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THE WHITE-CROWNED SPARROWS
(ZONOTRICHIA LEUCOPHRYS) OF THE
PACIFIC SEABOARD: ENVIRONMENT
AND ANNUAL CYCLE

BY

BARBARA D. BLANCHARD

CONTENTS

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BARBARA D. BLANCHARD

(Contribution from the Museum of Vertebrate Zoology of the University of California)

INTRODUCTION

THE SUBJECTS of this paper are the faintly distinguishable northern and southern coastal populations of white-crowned sparrows, *Zonotrichia leucophrys*, which have been given the subspecific names *pugetensis* and *nuttalli*. These occupy a continuous narrow band along the Pacific shore line of North America, and their breeding grounds are separated from those of the other races included under *Zonotrichia leucophrys*.

Several of the ensuing sections are concerned with the comparative physiology of the reproductive cycle and with its variations and their apparent natural control, as well as with the relatively minor aspects of behavior which, so to speak, float on the surface of the more deep-seated, cyclic pattern. This is not the result of interest either in the physiological or psychological details as such, but of conviction that comprehension, not of minor structural modifications but of the vital connection between the annual cycle and the environment, offers the most promising road to the center of problems of distribution and of potential evolutionary change.

Perhaps the greatest difficulty involved in such an approach is the discovery of a practical and workable instance of variation between populations which correlates with definable, broadly contemporary, and possibly dynamic conditions. In the discussion of geographic variations this consideration is rarely mentioned but must be paramount in any study which seeks the dynamic agencies behind variation and distribution. We are invariably ignorant of the age of any character and of whether it actually represents one branch of a simple, progressive, broadly contemporary split or a mere surviving remnant of ancient and irrecoverable fluctuations. "Subspecific" variation covers a multitude of stages and degrees of differentiation and antiquity and does not imply simple divergence at the fountain head. Probably, for a given species, the history of a group of variable populations would show a stream of very fluid minor characters. These may run parallel, diverge, cross, or recross, and their relation to one another at any given moment reveals little of their history. Many or most geographic variations, if indeed the products of external conditions, have probably outlived the conditions under which they were evolved and survive as vestiges or in process of transformation or obliteration. In many north-temperate latitudes during Recent time progress from environ-

mental diversity to uniformity seems to have been the rule rather than the exception; the migration of climates and floras, so well recognized by geologists and botanists, must have involved bewildering migrations and adaptations of faunas. Differentiating factors must disappear as well as accumulate; incipient characters must be absorbed as well as evolved; the geographic segregation of characters must be relaxed as well as enforced. Minor geographic variations, compared with more or less "specific" forms, are innumerable. Such variations, of which hundreds or thousands must come and go to one which points the way to lasting evolutionary divergence, must, in the long view—more especially in regions which felt the full capriciousness of the Pleistocene period—present a sequence of inextricable, kaleidoscopic confusion.

On the other hand, if the process of genetic shuffling is not altogether haphazard—if direct modification, segregation, or selection, by environmental factors or degree of enforced isolation, is to be detected—then assuredly an effort must be made to choose characters which seem to correlate with active recent and contemporary change as opposed to the indiscriminate heritage, whether in form or behavior, of past ages and vanished conditions. The criteria for such a distinction are few and doubtful. Among them may be the rudimentary character of the differentiae, the size of the coefficients of variation, the revelation of the course of the divergence through intergradation, the extent to which behavioristic or physiological characters appear to be adaptive to, or to correlate with, present conditions, or, very rarely, sharply defined endemism in areas only recently habitable. The cumulative effect of such considerations may, or may not, incline us to believe that we are dealing with an instance of living change rather than with dead vestiges of lost forms or aspects.

To take an admittedly rather extreme example, it would be quite futile to attempt to include another race of the same orthodox "species," *Zonotrichia leucophrys gambeli,* in the present study of divergence. Here intergradation and breeding-ground contact with the coast races have disappeared, morphology has achieved a uniform and widespread stability, and a series of sharply differentiated breeding environments (and doubtless equally distinct physiological and behavioristic patterns) have been assumed. We have not the slightest basis for a guess at what distance, perhaps in Tertiary time, the divergence began which has developed such distinct homogeneity and set off the Gambel sparrow from its ancient congeners. What intermediate fluctuations have taken place, or at what stages and under what conditions the elements of this more distinct and probably older pattern were combined, can never be deduced. It is equally doubtful whether present conditions have been dynamic factors or are narrowly essential to the present life cycle. Nothing could be more unsound than to interpret the present distribution and environment as generative of the characters of the present race.

In these respects the natural aggregates about to be discussed seem unusually likely to offer the results of a natural experiment under more or less definable conditions. Yet even here it is almost certain that the perfect moment for observation and measurement has passed. Even in these two confused

and sensitive, vaguely transitional, environmentally accordant, and morphologically feeble "races" it is more probable that something like re-unification has begun than that either is to continue its present visible progress on the long road to "specificity." Migration, once an essential condition to the use of the northernmost breeding grounds, can definitely today be dispensed with to the limits of the habitable terrain, and almost certainly it is being lost Similarly, numerous modifications of the physiology of reproduction in the North suggest a basically adaptive evolution in general accord with more boreal conditions and a briefer season than the most extreme present-day conditions represent.

Nonetheless, in broad outline and over the greater part of the range, the information so far accumulated conveys a strong sense of a series of life patterns formed in the mold of the present environment or, in the North, under slight modifications easily and justifiably reconstructed. The dynamic effects of the northern environment, if relaxing or relaxed today, are at least an affair of yesterday. Farther south, the fossil record, weak as it is, indicates a more persistent environment, older in its present guise and probably offering little contrast today to the conditions of the late Pleistocene. As far as actual degree of difference is concerned, it would be difficult to start at a lower stage and yet find unequivocal and measurable facts concerning the divergence and distribution of physiology and morphology.

Practical working conditions were unusually favorable. The birds are relatively easily observed, and the whole ranges, both breeding and wintering, are accessible—a far rarer situation here than in the Old World. Abundant material could be collected, and a quantity of accessory data is available on the topography, climatology, and botany of the Pacific coastal strip.

The general plan has been to assemble, rather blindly at first, the most complete picture possible of the year-round behavior and reproductive physiology of two populations, one migratory, the other resident, of widely sundered breeding areas, and to fill in the broader aspects of other populations, as opportunity served, in a far less intensive manner. Next in importance come the boundaries of the total range of the whole aggregate and the physical and floral characters of that range and of the marginal or closely extra-limital areas, especially such characters as seem likely to be capable of affecting the birds, either as to cycle or distribution. Great emphasis has been laid on the history of the male reproductive system as a slow and exquisitely precise timekeeper for individual, racial, and environmental comparisons. One consideration has been kept most constantly in mind: although minor morphological variations, whatever the mechanism of their production, are almost certain to appear meaningless, variations in the annual cycle and in many aspects of behavior are more likely to assist perceptibly in, or to interfere with, the process of living. These therefore constitute the first point of incidence of environmental change on the efficiency of the organism.

As was to be expected, the field tended to grow out of all measure, and the strictly distributional material and conclusions have been excluded from the present paper.

SYSTEMATICS

INTRODUCTION

In a broad sense this entire paper is devoted to the systematics of *nuttalli* and *pugetensis,* although the significant differences are those of behavior and physiology rather than of structure The external morphologic characters are so slight and show such wide variation even within a single local population, as well as intergradation between different populations, that it is impossible, by such means, to separate individuals except in the extreme groups of the range of variation. Differences in migratory instinct, however, times of recrudescence of the gonads, molt program, assumption of fat, and song patterns, are reliable criteria which distinguish the vast majority of individuals, at least of the extreme populations.

RANGE

BREEDING RANGE

The breeding and wintering ranges of the *nuttalli-pugetensis* group are indicated in figures 1–4. As Grinnell (1928) stated, the breeding range extends south from Comox, Vancouver Island, along the mainland of British Columbia
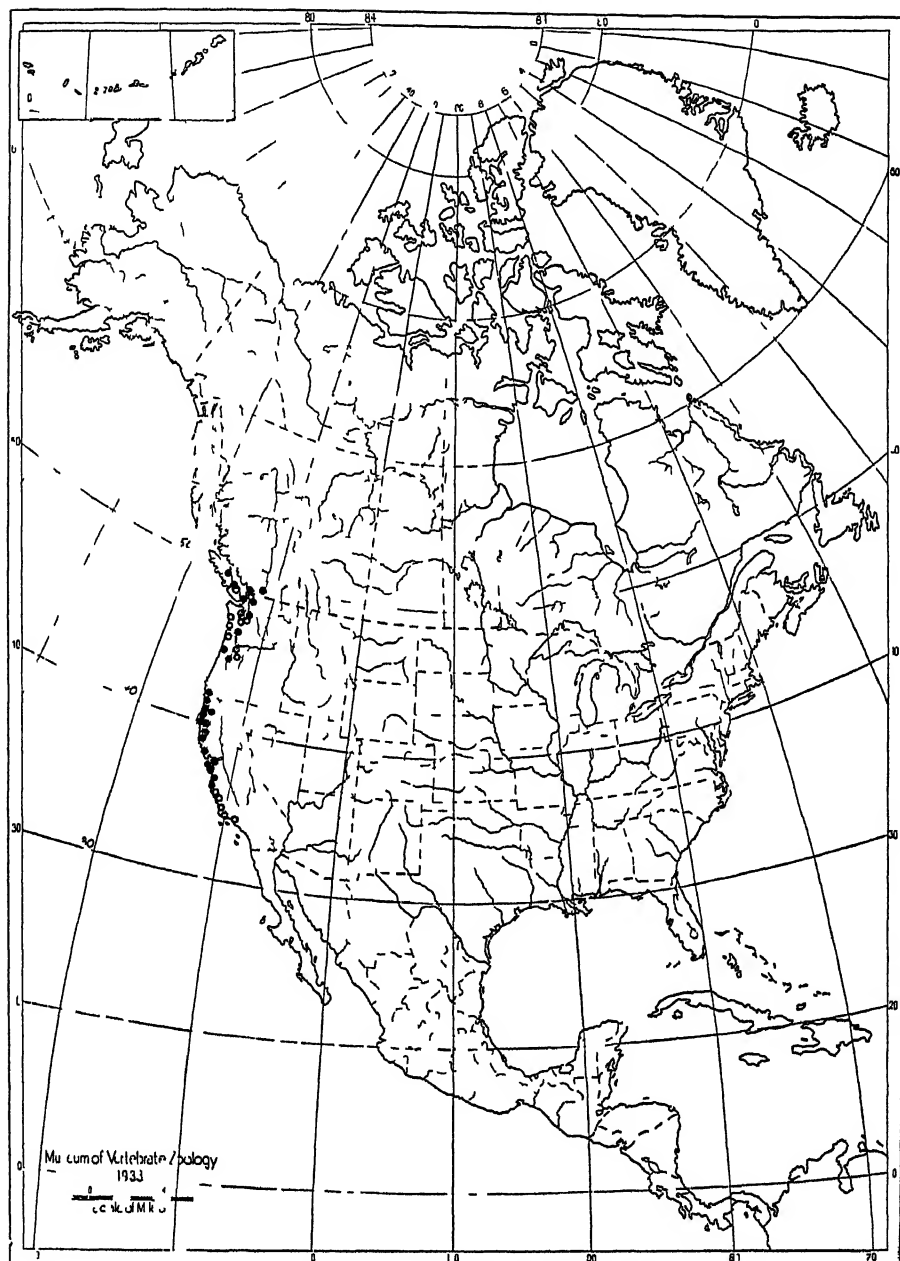
Fig. 1. Breeding range: *nuttalli-pugetensis.*

● = specimens.

○ = published reports.

/// = principal change in morphology.

\\\ = change from residential to migratory habit.

at the mouth of the Fraser River, through western Washington and Oregon, and along the coastal strip of California to Point Concepcion and casually to Santa Barbara.

On the map of the breeding range I have indicated two areas by diagonal shading. That from upper left to lower right lies between the southernmost point where I know the birds to be absent in winter and the northernmost point where I know the birds to be resident, and therefore represents the area of transition from migratory to nonmigratory habit. These limits were determined partly by field work in Oregon and partly by special observations made in the vicinity of Waddington, Humboldt County, in northwestern California in March of 1939. The area shaded from upper right to lower left indicates the strip within which the faint lightening of the general tone of the plumage, which is the chief morphological criterion, probably occurs. But since in any population the complete transition from one phase to the other is easily to be found, only a prohibitive amount of material, carefully spaced geographically, could define the precise nature of the morphological inter-gradation. The most that can be said at the present time is that the majority of the resident Humboldt County, California, birds are as light in color as those of any northern population, whereas those of Berkeley, California, are, en masse, decidedly darker.

Clearly, the variations in behavior and morphology do not coincide geographically. The profound distinction between migratory and nonmigratory habit does not accord with the nomenclatural division, so that part of the *pugetensis* population migrates distances up to a thousand miles, whereas the other is resident. This is the actual situation at present, if we are to retain the morphological concept of the races of Grinnell, who described the Puget Sound sparrow and reviewed the synonymy in 1928.

<div align="center">WINTERING RANGES</div>

Dr. Erickson and I devoted a week in December, 1937, to a search of the coastal regions of central and southern Oregon but found no Puget Sound sparrows north of Coquille on the seacoast or Umpqua toward the inland margin of the range. From these points south, however, as indicated on the maps of the wintering range, I found small flocks, and from the Oregon-California boundary line south to Carlotta, California, large flocks of thirty to sixty birds. This establishes fairly accurately the northern boundary of the winter range, although odd birds have been reported during midwinter at Tillamook and Portland, Oregon, by Mr. Reed Ferris, Mr. Alex. Walker, and Mr. Stanley Jewett; and even at Comox, Vancouver Island, the northern limit of the range, by Major Allan Brooks. Many wintering specimens of *pugetensis* have been taken in California south of the breeding range of *nuttalli;* a few have been taken at scattered points east of the Nuttall sparrows' narrow coastal strip.

Banded Berkeley Nuttalls remain the year round. All white-crowns of the *nuttalli-pugetensis* aggregate taken east or south of the California breeding range have turned out, if positively identifiable, to be *pugetensis.* The breeding population is resident through most of California.

Fig. 2. Winter ranges: *nuttalli-pugetensis*.

● = specimens or seen in field.

○ = published reports or correspondence.

MEASUREMENTS AND COLOR STUDIES

The measurements of skins are summarized in Appendix I. In addition to the material examined by Grinnell, I had new series of skins of breeding birds from six localities between Berkeley and Comox and large series of both races
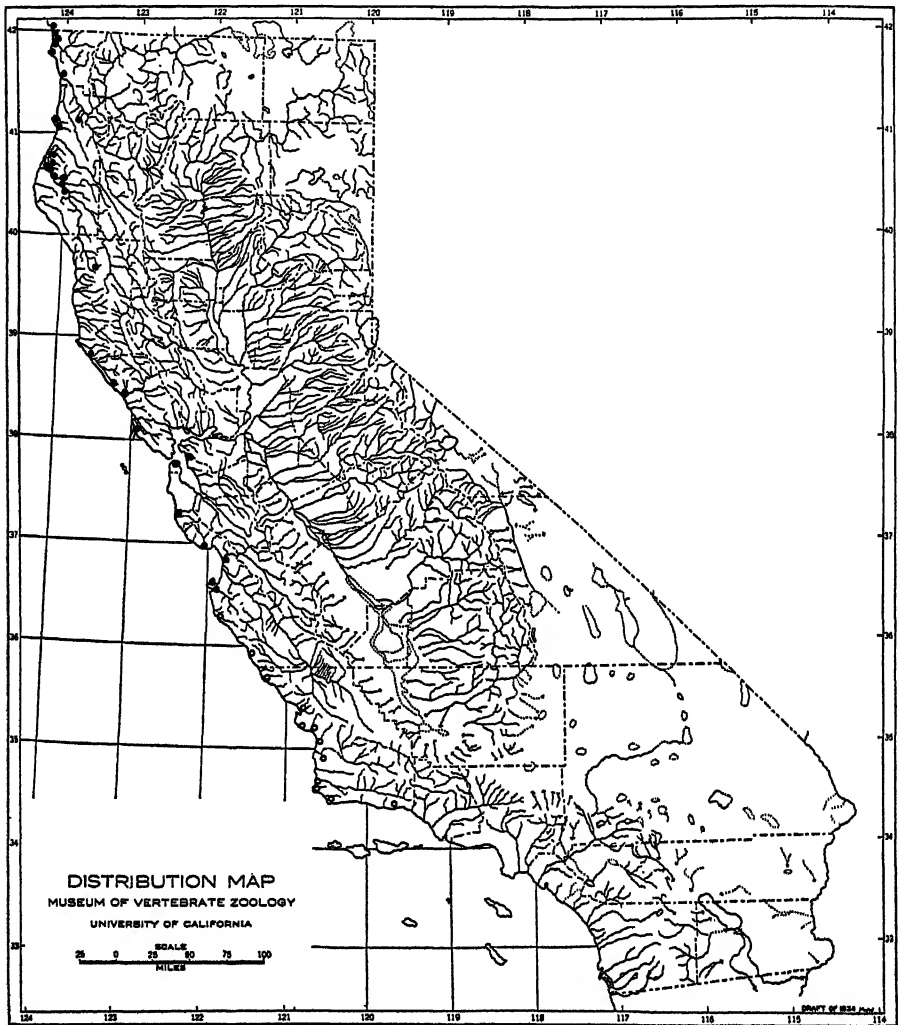
Fig. 3. Breeding ranges of *Zonotrichia leucophrys nuttalli* and *Z. l. pugetensis* in California. Solid symbols, specimens; hollow symbols, published reports.

from Berkeley. The measurements of each series were treated statistically, that is, the mean, the standard deviation, and the standard errors of both were calculated. In the formula for the standard deviation the denominator "n—1" was used. For series of 15 or more birds, the coefficient of variation was also calculated.

The only measurement which requires explanation is the ratio of the length

of the sixth primary to the length of the fifth secondary. These are, almost always, the longest primary and the shortest secondary and were measured on spread wings to see whether the wings of the migratory and nonmigratory populations differed in shape. Both were measured from the point where they enter the skin to their tips, in a straight line.
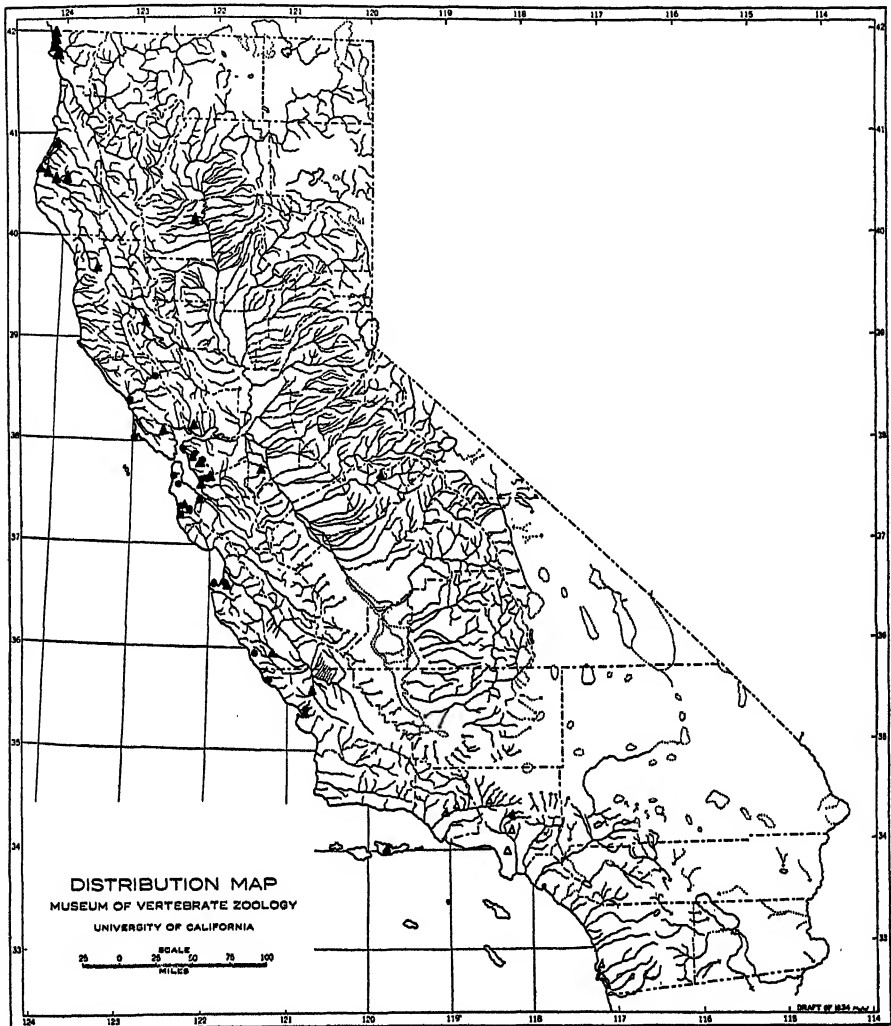
Fig. 4. Winter ranges of *nuttalli* (○) and *pugetensis* (△) in California. Solid symbols, specimens examined; hollow symbols, specimens reported.

In addition, I weighed most of the Berkeley sparrows and counted the numbers of wholly and partially white crown feathers on fifteen breeding males of each race. I examined the general color, and particularly that of the rump patch. A large number of individual contour feathers, especially from the dorsum, were mounted in rows on paper for the sake of the form, extent, and color of the markings.

Morphological Differences

SUMMARY

The only morphological differences I have been able to establish between the nonmigratory Berkeley population and the several northern migratory or nonmigratory populations are:

1. General lightening of color value in plumage of the northern populations. The rump patch is the most useful criterion.

2. A larger number of white and partially white feathers in the crown stripe of the breeding birds of the northern populations.

3. Lighter weight, perhaps reflecting smaller body size, but not reflected in the dimensions of the appendages, in the Puget Sound sparrows as compared with the Nuttall sparrows wintering at Berkeley.

DISCUSSION

1. Color of plumage. The northern populations are lighter in the color of all contour feathers. Although quantitative evidence is an impossibility, it is beyond question that in this respect the range of variation of the Nuttalls of the San Francisco Bay region is greater than that of any *pugetensis* population. This suggests that the Nuttall sparrows in question represent, not the typical or optimum region or metropolitan center of the southern populations, but an intermediate area of rapid geographic change. Unfortunately, there is no adequate series of skins from more southern localities, which might show greater stability of the darker phase.

2. Numbers of wholly and partially white crown-stripe feathers in 15 Berkeley and 15 Friday Harbor males chosen at random gave larger averages for the northern series. Numbers of wholly white feathers in *pugetensis* exceed those in *nuttalli* by about 18 per cent; numbers of partially white, by about 8 per cent.

The greater width of crown stripe in *pugetensis* can be seen better in the field than on dried skins, particularly just following the prenuptial molt. It was my observation of living birds in the field which suggested examination of this character. As might be expected, the birds which are paler in general body color also have more white feathers in the crown.

3. Weight. I was unable to weigh the birds collected at Friday Harbor or at any other northern stations. I am therefore reduced to the somewhat unsatisfactory expedient of using weights of the wintering population of Berkeley to represent the northern race. As explained later (pp. 83–84), the chances are large that these birds come from a far northern breeding ground.

Weights of adults and immatures are tabulated separately. It has been evident from the histories of large numbers of banded birds and from the examination of many autumn skulls that the brown or black-and-white heads are safe criteria of first-year birds or adults, respectively. A single exception is a banded bird, M.V.Z. no. 54481, collected by Mr. Ernest D. Clabaugh at Berkeley, which replaced the cranial black stripes with brown stripes when not less than one and a half years old.

For the male specimens I chose only those birds which were recorded as having no fat. For the females I included birds with little fat, since almost all females, both Nuttall and Puget Sound sparrows, have a small amount of fat in winter. The average weights of wintering birds are summarized in Appendix I, tables 12 and 13. A substantial difference between the races is shown by the adults of both sexes. The series of adult male Nuttalls averaged 2.59 gm. or 10 per cent heavier than that of adult male Puget Sound sparrows wintering at Berkeley. I lack sufficient weights of immature *pugetensis* to make a similar comparison. It is quite possible that, if the skinned bodies had been measured, corresponding size differences would have been found. This was not feasible, since it was necessary to open and preserve the carcasses with the greatest possible speed.

With the single exception of the weights of the wintering Berkeley populations, the quantitative data are purely negative and reveal no significant variability in size between any two populations.

DIFFERENCES IN EXTENT OF PRENUPTIAL MOLT

As indicated by Grinnell (*op. cit.*), the prenuptial molt is much more extensive in *pugetensis* than in *nuttalli*. In the former it involves all the feathers of the head and many of the dorsum, breast, and belly. In the latter it is confined for the most part to the anterior pileum and throat, although 7 of the 18 birds I examined which showed head molt had small patches of ensheathed feathers on dorsum or breast or both. In addition to these differences, I found that in *pugetensis* the deck pair of rectrices are often renewed, whereas in *nuttalli* they are not. Of 57 Puget Sound sparrows which were just finishing or had finished the molt, 22 had definitely molted the deck pair and 12 had definitely not done so. In the remaining 23 the deck pair were slightly worn at the tips, but, since these were all trapped birds, it was impossible to determine whether or not the wear was natural.

The difference in head molt accounts for the fact that the first-year Puget Sound sparrows breed in fully adult plumage, whereas first-year Nuttall sparrows breed in wholly or partially immature plumage. Of the 206 skins of breeding Puget Sound sparrows which I have examined, to say nothing of the hundreds which I have watched in the field, all but two have had fully adult plumage. In two skins a few black crown feathers had brown portions, though the vast majority of the feathers were pure black or white. Of the 79 breeding Nuttalls which I examined, however, 35 had wholly or partially brown head stripes.

There is wide variation in head patterns of the first-year Nuttall sparrows, which range from completely brown-headed birds to those with nearly all black and white feathers. Here, as in general color, the Berkeley Nuttall sparrows are far more variable than the northern birds. The first-year males have, on the average, more nearly adult plumage than do the first-year females. Of 14 breeding first-year males, 10 had a few, and 4 had a majority, of black and white feathers. Of 13 breeding first-year females, 3 had no black or white feathers whatever, 9 had a few, and only 1 had a majority.

CONCLUSION

The obvious anomaly in the comparison of these populations is the combination of such deep-seated differences in behavior and physiology with such vague and incipient differences in morphology. The impression of a very general fluidity, variation, intergradation—hardly more geographic than individual—leaves one with the impression that the process of differentiation is very likely to be incipient and active. There is no sense of final establishment, such as might be expected if the differentiation were residual, inherited from some previous period of longer and wider separation.

BEHAVIOR

INTRODUCTION

This section is devoted to the annual cycles of behavior in two widely sundered populations, one migratory, the other resident, taken as representative of the opposite terminal regions of the fifteen hundred miles of linear range It has two objects: first, to ascertain the precise respects in which the cycles differ, as a means of isolating the incipient tendencies to diverge that, probably in most geographic variations and almost certainly here, not only antedate duality of form or pattern but are far more apt to be comprehensibly connected with changing conditions of life. Second, to split up the complex change from wintering to breeding behavior into as many discrete elements as possible, which year by year can be used as points of reference for the comparison of the populations and the physical conditions of the environment.

The cycle in the Nuttall sparrow was worked out on the basis of a limited number of color-banded pairs studied for five years at Berkeley; that of the Puget Sound sparrow, by four years' study of the wintering flocks at Berkeley and one season's study of the breeding birds at Friday Harbor, Washington. In the spring of 1934, I trapped and color-banded seven pairs of Nuttall sparrows in the center of the University of California campus. I followed these as long as they survived, banding and watching whatever young and adults subsequently settled in the area to carve out territories or to mate with the bereft member of an established pair. The flocks of wintering Puget Sound sparrows were watched on wild land near Berkeley as well as on the campus. In early April, 1936, I went to Friday Harbor to await the main influx of breeding birds. I color-banded 32 adults within a day or so of their arrival and followed these and 16 others (24 pairs in all) until after the second broods had been fledged.

My methods of making the colored bands and of marking the birds were modified from those described by Erickson (1938, p. 250).

THE NUTTALL SPARROW

For convenience I have divided the cycle of the Nuttall sparrow into four phases: the base level of fall and winter behavior, the rising tide of territorial and sexual instincts, reproduction, and the subsidence of territorial and sexual instincts. These concepts are arbitrary, and the most refined histological or

behavioristic study justifies no such precise division. Elements of behavior are apt, as I have said elsewhere (Blanchard, 1936), to be not sharply sundered entities but recurrent manifestations of permanent instincts of variable intensity.

THE BASE LEVEL: BEHAVIOR IN FALL AND WINTER

The adults.—My banded pairs remained on their breeding areas through the fall and winter. Mates foraged and perched together and followed each other about, uttering the *eep* which serves as the location note. Both sexes sang sporadically, and an occasional territorial dispute involved forceful singing and chasing. The instinct to patrol the area was absent or nearly so, however, and several of the pairs were joined by flocks of immatures and, rarely, by mateless adults. These newcomers were treated with such complete tolerance that only the most careful observation could detect a certain aloofness as well as a certain dominance in the established pair.

Adults: restriction to breeding area.—During the fall and winter seasons of 1934 to 1937 I followed ten of the eighteen banded adults which bred in the same territory at least two successive years. Eight of these were paired; two (males VIII and XI) had lost their mates. I have 126 sight identifications between September 1 and January 1. These are listed in table 1. One hundred and seven records are of birds on their breeding areas, which varied in extent from .9 acre to 1.7 acres; 19 are of birds which had wandered a short distance (not more than 100 yards) into the territory of an adjoining pair. None was seen farther from its own area except one unmated male (XI), which was responsible for fifteen of the sight records in the second category. In winter he followed a group of immatures into the area of pair I, but was never seen farther than about 200 yards from his own area, to which he again restricted himself the next spring.

These records represent virtually all the attempts I made to find the birds. With rare exceptions, I found them readily within a few minutes after entering their breeding areas.

Since the adults stay on their breeding areas through the winter, it is natural that they should occupy essentially the same territories in successive years. This was true of 14 out of the 17 banded birds which I followed for more than one season on the campus. The exceptions were birds which shifted mates and territories in the midst of a breeding season and then stayed in the new areas during the winter, breeding there the next spring. Each of the eight banded pairs which were together at the close of one breeding season and survived to the next bred together again, six for two years and two for three years, before one or both members disappeared. This included female I and female III, simultaneous mates of male I in 1934, which stayed with him through the winter and bred with him again in 1935, disregarding a young male (mateless in winter and quickly losing a mate acquired in early February) which sang strongly in an adjacent territory. The data on permanent occupation of territory and retention of mates are discussed more fully on pp. 35–38.

Adults: song.—Song does not disappear. I have many winter records of full song by the male and, more rarely, by the female. It may be as loud, but never

as frequent, as in breeding time. On rare occasions I have even found two birds perched conspicuously, alternating in loud singing. For the most part, however, the song is weak and sporadic, uttered from the ground or from an inconspicuous perch. My records for male VIII in 1936 include all gradations:

August 30.—Male VIII alternates in singing with unbanded immature; song weak, sometimes complete, sometimes trill omitted.

September 5.—Sings loud complete song several times from perch in bare shrub.

October 3.—Perches conspicuously on top of sycamore and sings loudly; long intervals between song.

October 5 and 8.—Perches in sycamore and sings loudly every few seconds; song indistinguishable in force and frequency from that of breeding time.

October 17.—Sings fragment of song several times, then one complete song.

December 6.—Heard loud singing, but could not see bird. Male VIII emerges from heather bush, chases an unbanded adult, dives into shrubbery and again utters song, now weak and fragmentary.

The song of the female is identical in pattern with that of the male but is usually fainter, more rapidly uttered, and often incomplete. An exception, discussed below, was the loud persistent singing of female III, in September, 1935.

The song pattern is usually constant for a given adult but shows both individual and geographic variations. I have diagrammed (fig. 5) the three predominant patterns for the Nuttall sparrows at Berkeley, San Francisco, and Carmel, California, using the modification of A. A. Saunders' method devised by Miller (1931*a*). The first and second patterns are used by the Berkeley birds, although the first is by far the more common. The second is the predominant one for San Francisco, the third for Carmel. As might be expected from its greater complexity, the pattern of the Carmel birds shows more individual variation than do the other two.

Three other notes are given at all times of the year: a throaty warble which defies syllabification, given when two birds squabble over a morsel of food; the *ip*, which is uttered continuously as the birds are going to roost, or when they are excited by the presence of a person or animal; and the *cep* already mentioned. I have also heard the *ip* note given at other times when there was no apparent cause for excitement.

Adults: disputes.—With the exception of an occasional chase, I have seen only two disputes between adults during the fall and winter. One involved three unbanded birds; the other, an unbanded adult and female III, mate of the polygamous male I. The latter warrants description as a very unusual flare-up of what was probably a weak sense of territorial jealousy, not only on the part of a female but in the indifferent fall season. The immediate cause seemed to be the desire of both birds to feed on the same pyracantha berries. During early September female III had frequented a certain bush on the edge of her territory until, we may imagine, habit verged upon necessity and the spot was unseasonably invested with the power to stimulate possessive jealousy. On September 9 and 15 I saw her sing there several times. Her song was complete but weaker than that of her mate. On the morning of September 17 I found her there on the ground, singing as forcefully as any male in breed-

ing time. Then an unbanded adult in the same patch of shrubbery sang, somewhat less vigorously. This was male VIII, the neighbor on the east. They sang at one another for four or five minutes, shifting over the ground about six feet apart. Then the male chased female III around the edge of the shrubbery. She lit on the ground and both sang again. Another chase took place, then

TABLE 1

SIGHT RECORDS OF TEN ADULTS, SEPTEMBER 1 TO JANUARY 1

Adults	Year	Observations on Breeding Area	Observations in Area of Adjoining Pair	Total
Male I	1934–35	8	0	8
	1935–36	10	0	10
Female I	1934–35	2	0	2
	1935–36	7	0	7
Female III	1934–35	11	3	14
Male IV	1934–35	7	0	7
	1935–36	5	0	5
	1936–37	3	0	3
Female II	1934–35	4	0	4
	1935–36	4	0	4
	1936–37	2	0	2
Male VI	1934–35	8	0	8
	1935–36	1	0	1
Female VI	1934–35	8	0	8
Male VIII	1935–36	7	0	7
	1936–37	10	1	11
	1937–38	2	0	2
Male XIII	1936–37	5	0	5
Male XI	1935–36	3	15	18
Total	....	107	19	126

more singing. The next morning this was all repeated, but female III sang less forcefully. The same afternoon I found both feeding silently on the same berries two feet apart, and so for the next four mornings. Both sang occasionally, but I saw no more pursuits.

Adults: tolerance of immatures.—Small flocks of immatures often spent the fall and winter in the areas of my banded pairs. Pursuit of the young by the owners sometimes occurred, but for the most part the male was tolerant of the sojourning birds; indeed, the adult pair often foraged with them. Yet even then the paired birds were not quite undifferentiated elements of the

flock, for the young birds always gave them the right of way. Without making an attack, an adult frequently hopped straight at an immature, which always gave ground. In such flocks I believe that, unaided by the bands and adult plumage, I could have distinguished the landowners by their aggressiveness alone.
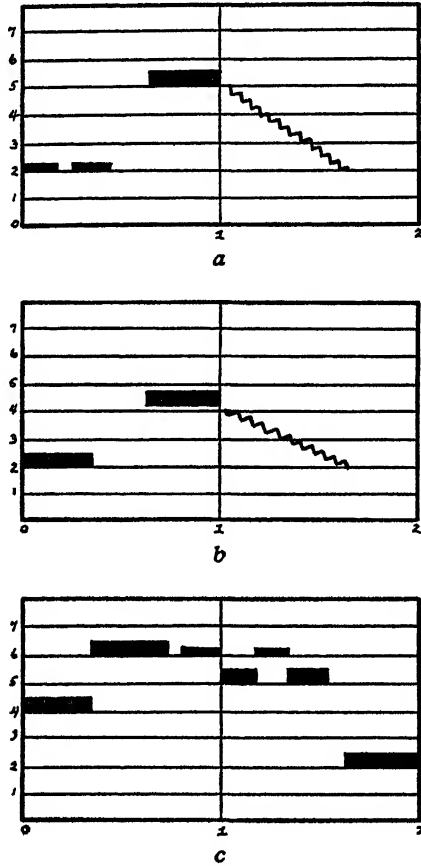
Fig. 5

Fig. 5. Diagram of song patterns of Nuttall sparrows at (*a*) Berkeley, (*b*) San Francisco, and (*c*) Carmel, California. Numbers on vertical scale indicate whole tones of pitch; numbers on horizontal scale indicate time in seconds. Thickness of bar indicates volume of sound.

Adults: discussion.—This evidence points to a more or less passive limitation of pairs to their breeding areas in winter, with almost complete tolerance of sojourning strangers and only rare flare-ups of jealousy between established neighbors. Restriction in winter is obviously not the product of conflicts between neighboring pairs; chasing, fighting, and patrol are almost completely absent. The attitude of the male toward immature and mateless birds gives us little reason to suppose that he would resent invasions of adjoining pairs if such occurred.

My tentative interpretation is that, on the campus at least, where food and shelter happen to be artificially maintained at uniform and constant abun-

dance, the relaxation of the territorial instinct results in less wandering or trespassing than might occur under the exigencies of wilder, more varied, and more capricious conditions. It is quite possible that on wild land, where grass and trees or shrubs are more unevenly distributed, there might be a greater tendency for adults as well as immatures to congregate in the more favorable areas. The fact that by continuous baiting of a single trap site on wild land I collected ten adult males between December 3 and January 16 of one year suggests that the group just described represents white-crown society in its most orderly aspect. It is inconceivable that such a series could be taken at one spot on the campus, even with the use of bait.

The immatures: flocking.—The immature birds travel in groups usually of three to ten birds, foraging silently or uttering the same *eep* used by the adults. When startled, the immatures react as one bird and fly to the nearest cover, but while foraging or progressing through the shrubbery, they show much less unanimity. The flock is not a closely coördinated unit but a loosely knit aggregate.

Immatures: restriction to limited area.—On August 26, 1934, I trapped within 400 yards of its birthplace, a young bird beginning its postjuvenile molt; it had been banded as a nestling the previous May. Through the following winter this bird (male XI) stayed with a flock of unbanded immatures within an area of 1.7 acres which included the spot where I trapped him and at the edge of which he settled the next spring. In October and November of 1935 I banded three immatures, two of which stayed near by the rest of the winter and bred the next spring within 50 yards of where trapped. One of these was retaken the following July less than 200 yards away. These histories, together with the fact that I had seen groups of immatures foraging day after day in the same spots, made me suspect that they, like the adults, might limit themselves to small areas in fall and winter.

To substantiate this, I color-banded fourteen immatures in August and September of 1936. All but one were seen again that winter: twelve, from one to fifteen times within 200 yards of where trapped, and one, once, within 400 yards. Eight settled the next spring on territories from 100 to 400 yards from the trap sites. None was ever found farther than 400 yards away.

Immatures: song.—The young birds begin to sing, though rarely, in mid-July, while still in juvenile plumage. This song may take the form of either a weak or abbreviated version of the immature song or a prolonged trill. As in most passerine birds, the immature song is much more variable than that of the adult. The young bird sings weakly, hesitatingly, often repeating notes of the first phrase before uttering the trill, which is sung so slowly that the separate notes can be heard. Every conceivable variation is used: the first three notes may be sung and the trill omitted, or one or more of the first three notes may be left out, and there are innumerable variations in the trill itself.

The immatures, like the adults, sing sporadically throughout fall and winter. The time of the transition to the fixed adult song must vary widely for different individuals; I have heard first-year birds sing the quavering vari-

able song as late in winter as January 9, but I have heard others sing like adults by November 10. I have never detected any connection between the assumption of adult song and territory establishment, such as Nice (1937, p. 59) found in young song sparrows. Almost all the immature birds which settled on the campus to breed were already using the adult song by early or middle January, when the establishment of territory began.

Immatures: disputes.—Pursuit is common among immatures in fall and winter. It is usually momentary, involving flock mates which may resume peaceful foraging a minute or so later. Sometimes, however, pursuit has been accompanied by loud singing and fighting, suggestive of a territorial dispute.

THE RISING TIDE OF TERRITORIAL AND SEXUAL INSTINCTS

Singing, chasing, and fighting.—The development of territorial jealousy has been analyzed in an earlier paper (Blanchard, 1936) but will be briefly reviewed here. The elements involved have been diagrammed for each year in figures 8 to 12. Between early and late January, depending upon the year, the first hints appear. The male sings more forcefully, more frequently, from a more conspicuous perch. He becomes less and less tolerant of the immature or mateless birds which have spent the winter in his area. When their song also rises in force and frequency, he pursues and attacks them until he regains sole possession of all or part of the territory he patrolled the year before.

With this achievement, if the male is already mated, song and frequent pursuits fall into abeyance, perhaps because there is no further need of them. Singing ceases for the present except for rare, weak, fragmentary songs. The immatures have segregated into pairs on their own territories. Settlement is now complete.

Yet these settled conditions do not prevent a new outburst at the beginning of incubation, with an even more continuous and regular outpouring of song and with the intensification or transformation of the instinct for defense into the habit of patrol. Some six to eight weeks after the cessation of daytime song, usually on the first day of incubation, the male's territorial behavior rises to a new climax. He sings loudly and persistently and patrols his area; that is, he flies from one tree to another on the periphery, stopping at each perch to sing. The instinct to chase and fight is still present but seldom exercised, simply because encroachments are rare.

In 1936 I had an exceptionally good chance to watch the development of territorial jealousy. All winter long, male ı had tolerated a group of eight to ten immature Nuttalls within his area. On the morning of January 9 I saw him perched on a bare sycamore with about seven of the immatures. He sang loudly several times, then stopped to preen his breast and flanks. Suddenly he started to chase two of the immatures, which had been perched within a few inches of him. I soon lost sight of all three, but I heard a cry as if male ı had caught up with one of the immatures and attacked it. A few moments later the whole flock, including male ı and his mate, were foraging peaceably on the lawn. Then I heard a weak quavering song from a Nuttall perched in a tall pyracantha several yards north. Immediately male ı flew to this tree,

displaced the singer, and himself sang loudly. The displaced bird moved only a foot but always gave way before male I as the latter shifted about, without actual pursuit. Then male I flew straight toward me across a wide lawn to a tall cedar, where he sang again. As he continued to sing I heard fragments of immature song, but he did not give chase again. Here were hints of all the elements of territorial behavior: advertisement by loud singing, territorial jealousy by chasing other birds, and patrol by flying to three conspicuous perches many yards apart and singing loudly from each one. For over two weeks these instincts came and went. Fits of territorial jealousy punctuated periods of apparent indifference when male I foraged peaceably with the flock or even let another male perch near him and sing. Frequency of song and pursuits increased until January 26 and then, as usual, subsided. On March 12, the first day of incubation, male I began to sing loudly every few seconds and patrolled his area.

In 1936 male I spent about 17 days in loud singing and in chasing and fighting. For the population as a whole, this period lasted from 22 to 28 days in the four years I watched. The interval from the day male I stopped loud singing to the first day he patrolled his area was 46 days; for the population as a whole this interval was about 45 to 58 days, depending upon the year.

The immature and mateless adult males usually get mates during the period of singing, chasing, and fighting. If they do not, they continue to sing after the mated males are silent. If a male loses his mate, he resumes loud singing and continues until another female joins him. The four unmated males which I watched rarely or never left their own areas when waiting for a new mate. Two adults, which waited six days and thirty days or more, respectively, before securing a mate, were seen and heard almost daily within their areas and never outside them. A third adult, male VII, which in 1937 waited over three months for a mate, was seen and heard regularly within a narrow strip of land between the territories of two mated males. Once I saw him enter the area of male IV, his neighbor on the east, and approach female IV*b* as if to copulate with her, but male IV immediately drove him out. In June of that year, as will be discussed more fully elsewhere, female IV*b* left male IV and mated with male VII. The fourth male, a bird-of-the-year which waited over a month after losing one mate and before getting another, stayed most of the time in his own area. He was seen, however, three times about 50 yards outside, twice in unoccupied pieces of land, once in the territory of an adjoining pair.

I have two records of females which lost their mates before the start of laying, one through an unknown cause, one through my interference. Each stayed on her own area and subsequently mated with a neighbor which already had one mate; the male then incorporated the area of the bereft female into his patrol. In 1936 female IV*b*, a bird-of-the-year which lost her first mate while she was building her nest, was annexed along with her territory within three days of her mate's disappearance, by male IV, already mated on an adjacent territory. Female XV, also a first-year bird, was left mateless when I collected male XV on February 22, 1936. Although at this time there was an

unmated male singing strongly about 125 yards away, female xv did not leave her area to join him, nor did he come to her. On March 3 I found male xi, already mated on an adjoining territory, following her about in her area. On March 22 I saw them copulate.

Trilling and posturing.—As soon as, or shortly after, the males begin forceful singing in January, the females begin to utter low metallic trills and flutter their wings. At first trilling seems to be called forth only by the loud song of a male (not necessarily of the mate) or by a chase or fight in which the mate is involved; it may or may not be accompanied by fluttering of the wings. As the season advances, trilling and posturing are almost invariably linked, and more and more often they occur independently of any apparent external stimulus. Both actions increase in intensity and frequency until the peak is reached just before copulation, in early to late March, depending upon the year.

I have fifteen records of almost identical behavior in males, several during border conflicts, others when the stimuli were not evident. I saw males trill and posture four times just after a fight, three times when neighbors approached each other but did not fight, once after a fight between two birds other than the trilling male, and six times with no special antecedent circumstances. I also saw one male trill and flutter its wings when a pair of English sparrows flew into the same tree. Trilling was usually as vigorous as by the female, but posturing frequently involved the fluttering of only one wing. One male, however, just after a fight, not only trilled and fluttered both wings but raised its tail, as do females before copulation.

Territorial jealousy in the female.—Except in instances of polygamy, territorial jealousy is not expressed by the female. Her weak song, which continues until nesting time, is not used for advertisement or warning, as is the loud song of her mate. I have never seen her join in a fight, and only rarely in a chase, in which her mate was involved. Her usual reaction under such circumstances is to trill and posture vigorously, a little apart from the conflict.

In polygamy, on the other hand, all the elements of territorial jealousy appear. The development of the territorial sense in the female independently of the male is illustrated in the behavior, in 1935, of females i and iii, simultaneous mates of male i. In winter both females made free of their common mate's territory, though with some tendency to localization. With the approach of reproduction, however, each female created for herself a subdivision of the main territory which she defended against the other female by loud singing and fighting, and in which she finally chose her nest site. From February 1 until late March, by which time both had nests, each female sang frequently from a favorite perch within her section. The two alternated in utterance, as do neighboring males. Twice, when female iii followed the male toward the section which belonged to female i, a fight ensued between the two females. They locked feet and jabbed each other on the breast. Then they separated, and female iii flew back to her section, while female i sang. Had they not been banded, I should have thought I was watching a boundary dispute between two males.

The singing and fighting of the females and the trilling and posturing of the males are merely two of many examples of a single response called forth in either sex by a wide variety of circumstances. Song, chasing and fighting, trilling and posturing, are manifestations of excitement; it is the observer's task to detect the source of the excitement which rouses the manifestation in question. Sometimes the connection is obvious, at other times obscure, as were once many aspects of song upon which Howard (1929) and others have since thrown light. Sometimes the manifestations are restricted to one sex, one season, and one source, stimulus, or apparent reference, but there is no manifestation which may not occasionally be brought out in either sex or by almost any stimulus at almost any time.

An illustration of this is the wing action described by Howard (*op cit.*, p. 36). "Both sexes of the Reed Bunting flutter their wings extravagantly during hostility . . . the Corn Bunting flutters his extravagantly during sexual activity. . . . We can neither recognize a bird nor its sex, nor tell the sort of situation that is in being, merely by wing-action."

This statement could also apply to song in the Nuttall sparrow. Song may by itself express, or accompany other expressions of, at least six unmistakable purposes or attitudes of mind: defiance or warning to territorial rivals, the longing for a mate, sexual excitement, concern for territorial boundaries (accompaniment of patrol), eagerness for the female's return to her eggs, and fright or physical shock. Examples of the first five have been, or will shortly be, given. I have two examples of the sixth (fright or shock). In the first, a male, which, when foraging with its mate, had dived into a clump of juniper, burst into song when I suddenly shook the shrub into which he had disappeared. The second was reported by Mr. Thomas L. Rodgers. While he was transporting Nuttall sparrows by car through several miles of city traffic, he noticed that each time he suddenly put on the brakes the sparrows, which were in darkened cages, would just as suddenly burst into song.

But song is far too flexible a language to be pigeonholed as a set of rigid significations. Many sporadic manifestations, perhaps best illustrated by night singing, are objectless or incomprehensible results of subjective or internal stimuli offering no external clues to their origins.

Relation to testis development.—The testis development of the Nuttall sparrow is analyzed in the next section (pp. 51–57), but certain correlations with behavior should be mentioned here. The beginning of increased and forceful singing and of chasing and fighting correlates with the time of increase in numbers of functional interstitial cells (histologic stages 3 and 4 of the testis as described later). The cessation of loud singing, when segregation has been achieved, occurs roughly at, or a short time after, the arrival of the testis at Stage 5 (when the interstitial cells no longer appear to be increasing in numbers and the tubules are filled with primary spermatocytes in synapsis). The ensuing interval of rare singing normally corresponds with the greatest and most rapid increase in the size of the testes, from less than 20 to over 100 mm.³, though this correlation is not requisite, since unmated males may sing throughout this period.

REPRODUCTION

The nest.—Nest building, carried on by the female alone, begins a few days before copulation, when trilling and posturing are reaching the climax.

Nest: site.—On the Berkeley campus all sorts of exotic shrubs were used for nest sites. Most of the nests were built in masses of low shrubbery a few inches inside the tips of the dense new growth and no more than arm's length from one edge of the clump. A few nests were in small isolated trees but always within a yard or so of more extensive shrubbery. One nest was built in an ivy vine on the side of a building; another, in the outer drooping branches of a tall acacia tree. The average height above the ground of 31 nests on the campus was 3½ feet, the two extremes, 1½ feet and 11 feet. Bolander (1906) found a few nests of Nuttalls in San Francisco on the ground and one at a height of 35 feet. One nest which I found on wild land was supported two feet above the ground by blackberry vines and the dead stalks of a composite and was surrounded by clumps of long grass, an echinocystis vine, and some small baccharis bushes.

Nest: material.—The platform of the nest consists of dried twigs from whatever plants are available. The middle layer consists of dead leaves, grass strands both dry and green, and small entire herbaceous plants. I have also found inch-long wooden splinters worked in. The lining is of fine dead grass stems and hairs.

Behavior at the nest.—The number of days spent in building the first nest of the season was from seven to eight or nine for the five nests found just as the female was starting to work. Three were worked on during parts of seven days; one, during parts of eight days; and one, eight or nine days.

The first hints of nesting are the interest of the female in material and the *ssseep* note of the male. I saw one female pick up a straw five days before she began to build; another began to gather material nine days before. At about the same time the male begins to utter *ssseep*. I heard one male use this note at least eight days before his mate began to build; another, probably seven days before; one, at least four days before; and one, the day before. It is used frequently when the female is actually building. The male perches near the site, uttering *ssseep* every few seconds as the female works. The suggestion is strong that the note may help to stimulate the female to build. If so, the male might influence, to a small degree at least, the time building is begun.

The elements of behavior which lead directly to building may reveal themselves several days before continuous work is begun, as the history of female I in 1935 indicates. I saw her pick up nest material for the first time on March 10. She was hopping about beneath the oriental thuja which was to serve as her nest site. She pecked at dried leaves, picked one up, dropped it. On March 13, I heard her utter a series of sharp *eep's*. This note is ordinarily given by the female Nuttall as she approaches the nest site with nest material in her beak. On this day, however, female I, although uttering the note, merely perched near the thuja without material. She protested with sharp *ip's*, as she saw me approach the thuja. On March 15, I watched her pick up a small piece of paper

and a strand of dead grass, fly with these to a perch on a twig of cotoneaster within a foot of the thuja, and there utter a series of *eep's*. Again she failed to enter the tree but remained perched on the cotoneaster, holding the straw and paper in her beak. Within a few minutes she flew to the ground and dropped the material. The instincts to pick up nest material, fly toward the nest site, and utter notes associated with nest building were all present but had not yet been synchronized into an effective procedure.

Two days later, on March 17, I saw her approach the tree with straws in her beak and utter loud *eep's* just before she entered it. Even then she did not work continuously but stopped after a few visits. Twice on March 18 I saw her approach the thuja with straws in her beak, only to drop the material without entering the tree. On the following day, March 19, these scattered impulses became merged and intensified in coördinated activity, and she began continuous work. By March 25 the nest appeared complete, though perhaps she added more material to the lining after this date.

The details of a single morning's work are best illustrated by the behavior of the same female the previous year. I watched her from 8:00 to 11:30 A.M. on March 11, which was the second or third day she had worked on the nest. At 8:00 A.M. female I and her mate were foraging near the nest site, a small oriental thuja within a few feet of which was a dense clump of cotoneaster and several small trees of pyracantha, thuja, and yew. Female I trilled and postured seven times as she foraged. At 8:15 she carried material to the nest, and from then until 11:30 built almost continuously, making 135 trips to the nest with material and stopping only three times, and then only for a moment, to feed. Almost all the material was gathered within a few yards of the nest; it consisted of dead twigs and leaves, strands of dry grass, pine needles, small green plants and fresh grass stems. Dead leaves and dry grass were brought most often. Only three twigs were brought, all within the first hour. Eleven trips were made with green plants and fresh grass, all during the last hour. After every few trips (on an average of every five) the bird could be heard fluttering on the nest, probably molding the cup.

I looked at the nest twice the same afternoon but saw no sign of female I. The next morning between 7:58 and 8:50 A.M. I saw her make nine trips. I visited the nest several times that afternoon but did not find her working. She spent parts of the next three days in building but never worked as continuously as on March 11. By March 15 the nest appeared complete. The other females which I watched also worked almost entirely in the morning.

Copulation.—Like territorialism and nest building, copulation involves the synchronization of several elements present for longer or shorter preceding periods. I have already described the gradual intensification of the female's interest in her mate as expressed by her trilling and posturing, which begins about six to eight weeks before copulation. The intensification of the male's interest, in so far as I can judge from his behavior, is much more sudden and rapid.

During January and February the male seems indifferent to the trilling and posturing of his mate. He pays no special attention to her other than to forage

with her and utter location notes as he has done throughout fall and winter. From early March on, however, he punctuates long periods of indifference by "attacks" upon the female. Suddenly, with no warning that I can detect, his indifference changes to aggression. He chases the female and jabs her with his beak. On March 14, 1936, male iv and both his mates (females ii and ivb) had been moving about together in the branches of the same tree when suddenly both he and female ivb uttered "squabbling" notes and he chased her over a wide road and landed on the pavement. They hopped together in the air and again landed on the ground, whereupon she crouched down, her back to her mate. He tugged at her rump feathers with his beak, bracing himself with his spread tail against the pavement. Then both flew across the road and perched in the same tree. I heard a few more squabbling notes, then all was quiet. Two minutes later the female was trilling and following her mate about close to her nest, which she finished building that morning.

I have seven records of such attacks, four of which took place from two to at least eighteen days before, and one, four days after, copulation. In 1936 (Blanchard, *op. cit.*) I was inclined to interpret the action as the male's attempt to copulate when the female was not yet ready, but this explanation no longer fits all the facts. In addition to the record of an attack four days after copulation, I have one (pair ii–iv in 1937) in which the female showed every evidence of being ready to copulate, but the male did not. The evening of the attack she had followed her mate about persistently, trilling and posturing continuously, but the male had paid no attention to her. Then suddenly both flew to the ground and the male attacked her.

Although this behavior suggests the "sexual flight" of the reed bunting as described by Howard, and "pouncing" in the song sparrow as described by Nice, I do not think it is strictly comparable to either. In both the reed bunting and the song sparrow these manifestations occur as soon as the female joins the male, whether this be two months or two weeks before copulation. The attack of the Nuttall, on the other hand, never occurs more than two and a half weeks before copulation, no matter how long the pair may have been mated.

The fact that the male reed bunting builds shells of nests early in spring, even before the female joins him, and that he pursues her in sexual flight as soon as she arrives, is presented by Howard as indication of the male's readiness to copulate as much as two months before copulation actually occurs. "Throughout the cycle the male is prepared to conjugate, but the female is under stricter physiological control." In the Nuttall sparrow at least, as will be shown more clearly in a later section, the male is under as strict a physiological control as the female, and the testes do not reach full breeding size until just previous to copulation. In fact, there is no perceptible interval between the attainment of breeding condition by the male and copulation.

Another change, which precedes copulation by from one to three weeks, is the beginning of evening song. During the half-hour before dark the male intersperses periods of foraging with faint singing, which seems to be directed at his mate rather than at neighboring males. Such song gains in force and

frequency until on the evenings when copulation finally occurs he follows his mate about, singing loudly both before and after he mounts her.

The behavior of pair XII on March 5, 1936, is characteristic of the period of copulation. At 6 : 05 P.M., when I began to watch, female XII was trilling persistently, fluttering her wings and raising her tail. The male uttered weak fragments of song and raised his crown. Both birds flew about fifty yards and landed in a pyracantha; then the male flew to a sycamore, and the female followed. Then both flew to the ground and copulated. The male approached again but did not mount, and a few moments later the female, pursued by her mate, flew several yards away, landed on the ground, and copulation again took place. The male then flew to a tree, sang loudly several times and, a moment later, when female XII flew into the same tree, mounted her three times. After several more flights followed by copulations, making eleven in all, both birds flew down to an alfalfa patch to forage.

At each copulation the male approached the female with his crown raised and tail lowered and spread, fluttered above her for about three seconds, then flew to a near-by perch. After copulation the female shook the feathers of her flanks and tail. Sudden straightaway flight of the female usually immediately preceded copulation.

Although at this period the male's attention centers on his mate rather than on the territory, he is always ready to drive out invaders. A striking example of this was the behavior of male VIII on April 15, 1937, when, during the half-hour before dark normally spent in foraging and copulation, he concentrated all his energies on driving out a strange, apparently unmated, bird. At 5 : 00 P.M. I heard male VIII alternate in singing with another banded bird, undoubtedly also a male, which had spent the winter in the area but which I had not seen since early January. This behavior of male VIII was in itself unusual, since at the copulation stage singing does not normally begin until later in the evening. From 6 : 35 P.M. until dark, at about 7 : 05, male VIII continually chased the lone bird, which again and again tried to sneak back into the area. I saw fourteen pursuits, each lasting from six to ten seconds. After each, male VIII perched conspicuously, his crown raised, and sang several times in rapid succession. The stranger, however, kept his crown lowered and was silent except for a single weak song. After he was chased to the boundary, he would wait a few moments, then fly back near where the owners were feeding. Several times he tried to avoid the male by diving under some shrubs in the center of the territory, but male VIII always followed and chased the intruder into the open.

Male VIII spent only five out of the thirty minutes in foraging. Each time he returned to the center of his area and started to feed, he would spy the stranger working back into his territory and would start another pursuit. Then he would sing for several minutes, apparently too excited to eat or to be interested in his mate. All evening she had followed him about, trilling and posturing whenever he sang. Once, before most of the pursuits, he copulated with her. Four other times he started to mount her, only to be interrupted by the return of the lone bird, which had the power to draw him away in immediate

pursuit. Twice, when female VIII started to fly away from him, he apparently mistook her for the invader and started to chase her, but stopped as soon as she landed on the ground and crouched in front of him.

This continued until almost dark. Then male VIII flew, without more foraging or attempts at copulation, to the incense cedar which served as his roosting place, and uttered loud *eep's*. The female, however, had not yet gone to roost, and the male flew out again, perched on a sycamore and sang. Then both entered the cedar and settled for the night.

Although copulation occurs most often during the half-hour before dark, it may take place at other times as well. I have twenty-four records of copulation, one at 6:50 A.M., one at 8:55 A.M., one at 4:45 P.M., and twenty-one between

TABLE 2

NUTTALL SPARROWS: CLUTCH SIZE AND TIME OF YEAR

Month	Number of Clutches				Total Number Clutches	Average Number Eggs per Clutch
	2 eggs	3 eggs	4 eggs	5 eggs		
March...............	3	6	1	0	10	2.8
April................	2	58	21	0	81	3.2
May.................	2	18	19	1	40	3.7
June................	0	12	1	0	13	3.1
July................	0	3	0	0	3	...
Total...............	7	97	42	1	147	3.25

6:00 and 7:00 P.M. The number of times I saw the same pair copulate in one evening varied from once to eleven times. The average of twenty-one records was five times. I have two records of copulation for the same pair six days apart, for another pair, four days apart, and for a third, three days apart. It is probable that they also copulated on the intervening evenings.

As for the relation of copulation to nest building and egg laying, I have records of copulation from two days before to four days after the female begins to build and from four to fifteen days before the first egg is laid. For nine pairs, the interval between beginning of the nest and first observed copulation averaged 2.1 days; that between first copulation and first eggs, 5.9 days.

Eggs: time of laying.—From one to seven days after the nest is completed (an average of 3.6 days for 12 records) and from four to nine days after first observed copulation, the first egg is laid. Eggs are laid on mornings of successive days until the clutch is complete. I have records of the time of laying of six eggs, three of which were those of the second clutch, and for three of which the clutch number was not known. Five were laid between 6:00 and 6:30 A.M., one, between 6:15 and 6:58 A.M. I have less exact records for fourteen others, nine of which were laid at least before 8:50 A.M.

Eggs: number.—The number of eggs per clutch varies from two to five; the average of 147 sets is 3.25. As Erickson (1938) found in the wren-tit, the size of the set in the Nuttall sparrow is apparently influenced by the time of year

it is laid and by the age of the female. In general, the later the season, up to June, the larger the average clutch size. Females two years old or over lay on the average slightly larger clutches than first-year females (3.29 eggs per clutch as opposed to 3.00). These facts are given in tables 2 and 3. Table 2 summarizes my data for sets found in Berkeley and also data kindly furnished me by Mr. Henry W. Carriger, Mr. Dudley S. De Groot, and Mr. W. E. Unglish, for sets collected at Lake Merced and other points near San Francisco, and Watsonville. Table 3 is based entirely upon my own data.

As table 3 indicates, both first and second clutches may consist of from two to four eggs, though the second clutch averages a little larger. First clutches laid in April average larger than those laid in March. Of ten first sets laid in

TABLE 3

NUMBER OF EGGS IN SUCCESSIVE CLUTCHES IN A SINGLE SEASON

Clutch	Number of Clutches			Total Number Clutches	Average Number Eggs per Clutch
	2 eggs	3 eggs	4 eggs		
First clutch..........	4	15	5	24	3.04
Second clutch.......	1	2	7	10	3.60
Third clutch.........	1	3	1	5	3.00
Fourth clutch........	..	3	..	3	3.00

March, only one had 4 eggs. The average was 2.8. Of fourteen first sets laid in April, four had 4 eggs each, and the average was 3.2.

I have records of all clutches laid by female 1 for two years. In 1934, when she bred for the first time, she laid four clutches of 3, 2, 2, and 3 eggs each. In 1935 she laid four clutches of 2, 4, 4 and 3 eggs each.

Incubation: duration.—Incubation is carried on solely by the female. Its beginning in relation to egg laying varies. Five females began on the day before the last egg was laid, five, on the day the last egg was laid, and one, the day after. In terms of clutch size, 3 females with sets of only two eggs all started the day the second was laid. Of 5 females with sets of three eggs, 3 started on the day the second was laid; 1, on the day the third was laid; and 1, the day after the set was completed. Of 3 females with sets of four eggs, 2 started on the day the third egg was laid and 1 on the day the set was completed.

The average time of hatching for ten sets of eggs was twelve to twelve and one-half days after the first day of continuous incubation. One set hatched in eleven or twelve days; two, in fourteen days. The rest hatched at the average time.

Incubation: behavior of the female.—The female sits on the eggs for periods averaging about twenty minutes each, then leaves the nest to forage for intervals of about seven minutes. When the female forages, she hops about hurriedly, covering a large area of ground in the few minutes she stays off the nest. This rapidity of movement is so characteristic of the incubating female

that I have, on that basis alone, correctly predicted that a given female had started to sit on eggs.

Each time the female leaves or returns to the nest, she utters the same strident *eep* she used when building. If I disturb her on the nest, she hops off without a sound and drops down through the surrounding foliage. If it is early in the incubation period, she starts to forage in a minute or so; if late, both she and her mate become much excited and protest with loud *ip's*. Once, as I looked into a nest, one of the pair flew directly at me, almost touching my face. This reaction is more common, however, after the young hatch.

The female's position on the eggs is similar to that described for the wren-tit (Erickson, *op. cit.*, p. 289), with the tail raised at a sharp angle and the chin resting on the edge of the nest. Owing to the denseness of the shrubbery in which the nests were built, I could not watch the female for more than a moment without disturbing her and therefore do not know how she turns the eggs.

Incubation: behavior of the male.—As has been said, on the first day of incubation or a day or two before, the territorial behavior of the male reaches its highest development. His attention, centered during the period of copulation chiefly on the mate, now shifts to the territory, which he guards by loud, continuous singing and patrol.

Unlike the song sparrow (Nice, 1937, p. 126), the male Nuttall sparrow does not regularly call the female off the eggs, nor does he guard the nest in her absence. He sings at varying distances from the nest and may or may not be near it when the female leaves. Often he stops singing to forage with her, and the pair may wander more than a hundred yards from the nest. However, he may be involved, in some degree, in her return. He is, at least, keenly aware of it, and probably somewhat concerned in it. The female may return alone but more often is accompanied by her mate. Sometimes she is the first to stop foraging and flies toward the nest, followed by the male, which perches close by and sings. At other times the male finishes first, flies to a perch near the nest and sings, whereupon the female gradually comes nearer and nearer and finally resumes incubation.

Under these circumstances we can only speculate as to the degree to which the behavior of the male may operate to suggest or hasten the female's return. I have one record of a male which definitely urged a reluctant female back to her eggs. In 1937, female XVII, a first-year bird, built her nest about ten feet above the ground in an ivy vine on the side of a building. I watched her for thirty-five minutes on the morning of March 27, which, judging from the time the eggs subsequently hatched, was probably the first day of incubation. At 9:55 A.M. I found her mate singing loudly a few yards away from the nest. At 10:00 the female joined him and both foraged. A few minutes later, she flew into an acacia tree, a branch of which extended to within a foot of the ivy which held the nest. She hopped from one branch to another, "pointing" toward the ivy and uttering *eep's*. The male flew into the same tree and also faced the ivy. He hopped just behind his mate, almost touching her with his breast, until she was within a few inches of the nest. Then he flew a few yards off and sang. But as soon as he left her, she flew down to the ground to forage,

and the male quickly joined her. Both soon returned to the acacia and repeated the same performance four times. Once she went as far as to flutter in the ivy above the nest, only to retreat to the acacia and then to the ground. A half-hour after I had begun watching, she again approached the ivy and, after much hesitation, entered it. The male had stayed close by all this time.

Six days later I watched the same female, this time unaccompanied by her mate, approach and retreat from her nest for over an hour without entering it. All this time the male never came near the nest but sang every few seconds from the southwest edge of his territory, some 125 yards away. After making over fifty unsuccessful attempts to go to the eggs, the female finally gave up and flew off to forage. I am sure that her reluctance was not the result of my presence.

Hatching.—As might be expected from the individual variation in the beginning of incubation, the eggs of one set may hatch either all on the same day or on two successive days. The longest intervals between first and last hatchings of eggs in one set were somewhere between 7 and 15 hours for a set of three eggs, and between 16 and 17 hours for a set of four.

As Miller (1931*b*) found in shrikes, the eggs in any one set do not necessarily hatch in the order they were laid. In 1934 the marked eggs of a Nuttall sparrow in a set of three all hatched on the same day: number 2, first, by 5:50 A.M.; number 3, next, by 7:00 A.M.; and number 1, last, by 11:45 A.M. In two clutches of four, the last egg laid was the last to hatch. In one of these, the first and second eggs laid had hatched by 2:50 P.M.; the third, by 4:20 the same day; and the fourth, between 7:00 and 7:55 the next morning. In the other clutch, eggs 1, 2, and 3 hatched between 7:10 P.M. of one day and 6:30 A.M. of the next, and egg 4 hatched before 4:45 P.M. of the second day.

Young: behavior of adults.—On the day the young hatch, the adults follow essentially the same routine as during incubation. The female now alternates between brooding the young and gathering food for herself and them. The behavior of the male is definitely affected and reflects awareness of the event. He continues his patrol but spends more time near the nest. If I appear while he is away, he responds at once to the *ip's* of the female by flying straight toward the nest and scolding. If I go straight to the nest, both birds change to a faint *tit* note, the chief function of which at this stage seems to be to warn the young. By the time the nestlings are seven or eight days old, they respond to it by stopping their food cries and crouching down.

For at least the first three or four days the female bears almost the whole burden of feeding the nestlings. I have seen her start to gather insects within two hours after the young hatched but have never seen the male visit the nest until the second or third day, and then relatively rarely. I kept track of the activities of one female on the morning of June 21, 1935, when her two young were about 24 hours old. Between 8:20 and 11:35 A.M. she left the nest eight times, on an average of every 16.8 minutes, and returned on an average of every 6.1 minutes. On her return I could usually see something in her beak, but it was not possible to watch her feed the young. Between 3:55 and 4:55 P.M. on the afternoon of the same day she averaged 10 minutes on the nest to

each 7 minutes of foraging. During the four hours I watched, the male came only once to the nest tree, then stayed so short a time that it is doubtful if he fed the young.

At such times as I did see a male feed the nestlings soon after they had hatched, he never went directly to the nest but carried the food to a perch near by and held it in his beak for as much as an hour before feeding it to the young. On the morning of June 30, 1935, I found male IV perched with a worm in his bill near his nest of day-old young. After nine minutes he started toward the nest but was interrupted by the female's return and retreated, still holding the worm. In fourteen minutes, when his mate again left the nest, he had another chance to feed the young, but he continued to hold the worm in his beak until her return twenty-one minutes later. Finally, an hour and twenty minutes after I began watching, I saw him carry food to the nest.

Although I have never seen either parent carry fecal sacs away from the nest, this has been reported by other observers, including Mr. Laidlaw O. Williams, who photographed a female with a sac in her beak (plate 3*b*).

The sixth day after hatching is the last on which I have found a female brooding her young during the day; only rarely have I found one sitting on the nest in the daytime after her young were four days old. One female brooded her nestlings each night until the eighth day after they had hatched. On the fifth night she still sat in the nest in a half-crouching position, but from the sixth night on, she perched on the edge of the nest and leaned over the nestlings, touching them only with her breast.

Young: development.—The young bird just after hatching weighs a little over 2 gm. It has down on the head, dorsum, wings, and thighs; this dries in about two hours and stands straight out from the body. The remnant of the yolk stalk is still visible, and the viscera can be seen through the transparent skin of the abdomen. The bird breathes spasmodically, the entire body throbbing. It responds to jarring of the nest by raising its head and waving it about unsteadily, the mouth wide open. At first it holds this position only for a moment before its head drops forward and the "egg position" is resumed (plate 2). I can hear no sound even when the beak is wide open. One nestling, less than 24 hours old, when rolled on its back, kicked feebly but could not right itself.

By the day after hatching, the juvenile feather tracts can be seen through the skin as dark pigmented strips. The bird has nearly doubled its weight and squeaks faintly. By the third day after hatching, the sheaths of the primary flight feathers protrude above the surface of the skin, the eyelids show a slit about a millimeter long, and the bird can right itself. The reflexive grasping of the nest lining by the feet begins at about four days after hatching. By the fifth day, the primaries are about seven millimeters long, and the eyes are wide open. The instinct to press the chin against a solid object was first noticed on this day, and from this time on the young hold their heads up, resting the chin against the nest or another nestling.

By the sixth day the primary sheaths are about eighteen millimeters long, but none has ruptured. The birds cry loudly enough to be heard ten feet away.

On the seventh day the sheaths of the primaries and the primary coverts start to rupture, and by the ninth day the vanes begin to uncurl. By the tenth day, when the young normally leave the nest, the feathers cover the body.

I weighed four broods of nestlings as soon after hatching as possible, and at approximately twenty-four hour intervals thereafter. Nest mates were marked by clipping a different claw on each. The weights are given in table 4, where the nestling numbers indicate the order of birth. The weights of nest mates usually accord with the order of hatching, that is, the oldest nestling

TABLE 4

Weights of Nestlings

Pair	Nestling Number	Day Hatched		Days after Hatching								
		Age in hours	Weight in grams	1	2	3	4	5	6	7	8	9
				Weight in grams								
I.....	1	2	2.3	4.4	6.0	8.8	11.5	14.9	17.6	19.6	20.8	21.6
	2	2–	2.3	3.9	5.4	7.7	10.2	13.7	16.5	19.6	20.6	21.5
III...	1	2–	2.1	4.0	5.7	8.1	12.1	15.2	18.7	19.8	21.8	....
	2	1–	2.1	3.7	5.5	7.8	11.1	14.2	17.3	19.8	20.5	....
	3	...	...	3.2	4.5	6.8	10.3	12.8	15.7	17.4	18.6	....
XI...	?	...	...	4.0	6.0	8.3	11.3	14.3	16.7	16.8	17.3	....
	?	...	...	3.4	5.7	7.7	10.8	14.1	17.5	18.4	....	....
	?	...	...	3.0	5.1	7.2	10.0	13.5	16.5	16.5	18.0	....
I.....	1	2+	2.8	4.6	7.0	9.8	11.9	16.3	17.1	....	....	....
	2	2–	2.1	4.1	6.2	9.0	10.4	13.5	17.0	....	....	....
	3	1–	2.2	3.8	5.8	8.4	10.4	14.3	17.7	....	....	....
	4	...	...	2.9	4.6	6.8	8.6	11.4	14.1	....	....	....

is usually consistently heaviest. This was not always true, however, since nestling 3 of pair I caught up and passed nestling 2 on the fourth and fifth days, and on the sixth weighed more than nestling 1. In the brood of pair XI, the nestling which was second heaviest for the first five days became the heaviest on the sixth day. I did not weigh the nestlings after the eighth or ninth day, since as soon as I touched them they jumped out of the nest.

Young: fledging.—The young normally leave the nest when about ten days old. Of 12 broods for which I have the dates of fledging, 8 left when all, or all but the youngest, were ten days old, 3 when eleven days old, and 1 when only eight days old. It is highly probable that the latter were frightened and left prematurely. Two other broods left when not more than ten days old, and one, when not more than eleven days old.

In 5 broods of two or three birds each, all nest mates were known to have left on the same day. In 6 broods, 3 of which had four nestlings each, at least one bird stayed in the nest after the others had left. This is what might be expected if one bird hatched a day later than its nest mates. In one brood of

four, three had left by 5 : 00 to 6 : 00 P.M. of one day, the fourth by 6 : 00 A.M. the next.

I have two records of nestlings which hopped back into the nest on the day they had left it. By 5 : 00 P.M. on April 17, two nestlings of a brood of three had left. The next morning at 6 : 00 A.M. I found all three back in the nest. When I looked at 5 : 15 P.M., all had left. In another brood, one bird left ahead of the other three but was back in the nest the same evening.

When the nestlings of one pair jumped out of the nest, they uttered a rapid series of *teez's* which brought the parents at once. The latter showed no fear of me ; they flew within a few inches of me to the nest and uttered strident *ip's*. When one fledgling hopped out into the open, one of the parents flew to it and drove it back to cover. The behavior of both parents and young of a brood which were fledged at the average age was essentially the same as that just described.

The first few days after fledging, the young perch in the shrubbery near the nest. They are usually so well concealed and respond so quickly to the warning *tit* of the parents that it is impossible to see them. The male now shares about equally with his mate the work of feeding the young. When the parents bring food or come near them in foraging, the fledglings utter *teez* and flutter their wings.

By the third to seventh day after fledging, the young of seven broods which I followed had moved to clumps of shrubbery some distance away from the nest. This must have involved crossing several yards of open grass—whether by hopping or flying I do not know. I suspect by the former method, since my earliest records of flight are for birds which had been out of the nest from seven to ten days.

When the young of the first brood are about twenty days old, the male takes over most of the task of feeding them. By this time the female has usually begun to work on her second nest. When from twenty-five to thirty-one days old, the fledglings forage for themselves but still beg food from the parents. The adults continue to feed them a little longer but soon ignore their persistent *teez* and may even chase or fight them. The oldest fledgling I have seen fed by a female was thirty-two days old, the oldest fed by a male, thirty-five days. Once I saw a female fight with her thirty-five-day-old fledgling; the next year I saw this female chase away another of the same age.

At about this time the young start to wander outside their parents' territory. At least by the time they are forty-eight days old they leave it forever. None, not even those which spent the winter only a few hundred yards away, has ever been seen again in its parents' area.

The history of one brood after fledging can be summarized as follows : In 1934, two of the three nestlings of pair II left the nest when between ten and eleven days old, either late on May 3 or before 8 : 00 o'clock the next morning. The third was still in the nest when I looked at 8 : 00 on May 4. By 12 : 30 that afternoon the nest was empty, and the brood had moved about five yards through the clump of juniper to the edge opposite that where the nest was built. That evening I found the brood in the same spot. One of the young

allowed me to come within two feet of it, then hopped out of reach. Three days later I found the young still there.

By May 10, when the fledglings were sixteen days old, they had moved about twelve yards across an open space to another clump of juniper. One fledgling perched quietly as I came near but, as I reached out my hand, flew to a tree about six feet away. Eleven days later, when the young were twenty-seven days old, I found them in approximately the same place. They still seemed entirely dependent upon their parents for food. I watched the male feed one fledgling a long worm, which he first broke into pieces by lashing it from side to side. The young bird made no attempt to pick up the bits from the ground but uttered *teez* continuously and waited for the male to shove the pieces into its beak.

On May 25, when the fledglings were thirty-one days old, I saw one foraging independently. The next day two had crossed a broad road on the west edge of their parents' area and were foraging with two unbanded young. Two days later I saw one fledgling for the last time in the parents' territory. On June 11 I found one, then forty-seven days old, about 200 yards away in company with seven other young Nuttalls.

Young: individual histories.—Of the fifty-eight nestlings which were banded and successfully fledged, only twelve were seen or reported after they left the parents' territory. One, hatched July 11, 1935, was shot the following April, at least a mile and a half from its birthplace. The others were found on the campus. Six were seen one or more times, from a week to six months after fledging, all within 350 yards of where hatched. One, hatched May 6, 1937, was collected nine months later, and would undoubtedly have bred, about 400 yards from its birthplace. Four bred on the campus, within 200 to 525 yards of their parents' territories.

It will be remembered that on August 26, 1934, male xi, when just beginning its postjuvenile molt, was trapped in the area where it was to spend the winter and at the edge of which it was to breed the next spring. Another young bird, banded in August, 1936, also when molting from juvenile to first-winter plumage, stayed throughout the winter within 200 yards of the place I trapped it. Two others, banded the same day and also molting, bred the next spring from 200 to 400 yards of where they had been trapped. These examples, together with those already discussed in the section on restriction of immatures in fall and winter, suggest the possibility that such wandering as is done by the young of the year may be confined to the period preceding the postjuvenile molt. However, unlike young song sparrows, which may take up territories the first fall (Nice, 1937), no proclamation of territory is made by the Nuttalls until the next spring.

Second and third broods.—By early to late July of each year, before the regression of the gonads began, all pairs had attempted to raise at least two broods. During the three years when I watched continously, one pair fledged three broods in one season, three pairs fledged two broods each, five fledged one each and tried until late June and early July to raise a second, and two made several attempts but failed to raise even one. Of eight pairs in which

the female or both male and female disappeared during the breeding season, three had fledged one brood each, one had made two unsuccessful attempts, and four had made one attempt before one or both members disappeared.

The pair with three broods fledged the second on May 27 and so had time before mid-August, when the molt began, to raise a third brood and care for the fledglings until they became independent. The three pairs which raised two broods each fledged their second on June 6, June 23, and July 21, respectively, and made no further attempts. At least two of these pairs would have had time for a third brood, had they not lost one or more broods between fledging their first and second. However, since casualties to the young were numerous in every year, it is probably safe to say that only very rarely would a pair be able to fledge three broods in one season. Of thirty broods of nestlings which I followed, only twelve were successfully fledged. The remaining eighteen died or were destroyed before leaving the nest.

From 14 to 29 days after the fledging of one brood (an average of 20 days for six records), the first egg of the next clutch was laid. For the pair which raised three broods, this interval was 14 days between fledging of the first and beginning of the second, and 20 days between the second and third.

For the second brood the nesting cycle follows essentially the same course as that described for the first, except that the male sings throughout the day and the female trills and postures much less frequently. This is interesting in reference to the suggestion of Howard (1929, p. 37) that "bodily movements are in inverse proportion to the intensity of the feeling." Trilling and posturing are most frequent and intense just before first copulation occurs, but decrease in intensity once full breeding condition is attained and both birds are ready at almost any time to copulate.

I suspect that the interval between completion of the second nest and laying of the eggs is shorter, but my data are insufficient to provide proof. For two females this interval was two days and three days, slightly less than the average (3.6 days) for the first brood.

If a clutch or a brood of nestlings is destroyed, a new nest is started within a few days. Three females began work on new nests within two or three days after their eggs or young had been destroyed. One female whose nestlings died four days after hatching started a new nest six days later. Another, whose eggs had well-developed embryos which failed to hatch, deserted them on the thirteenth day of incubation and nine days later began work on another nest. Under these circumstances the female takes less time to finish the nest and lay the first egg than she does for the first clutch of the season. The interval between the time one nest of eggs or young was destroyed and the first egg of the next clutch was laid was from 5 to 15 days, or an average of 7.5 days for six records. Since the females probably waited at least two days before starting to build, they averaged not more than 5.5 days for the same procedure which at the first of the season required an average of 10.6 days. This is what might be expected if, as I can show to be true of the male, there exists in the female a primary connection between stage of gonad development and degree of intensity of sexual behavior.

THE EBB: SUBSIDENCE OF TERRITORIAL AND SEXUAL INSTINCTS

In late July and early August, when the testes are rapidly regressing, the postnuptial molt begins. The birds become much less active and almost completely silent. Contrary to all probability, the time spent in feeding appears to decrease since it was almost impossible to find even those individuals whose forage routes I knew well. Trilling and posturing, chasing and fighting cease. As a general rule, singing also stops, though I have one record of a loud and complete song from a male which was molting heavily.

Even though all external manifestations of territorialism are suspended, a definite interest in the breeding area must persist. Two molting adults, which I trapped and carried a mile distant before releasing, returned to the trap site before they finished the molt. One was collected, but the other was still resident on its previous breeding territory five months later. On August 14, 1935, I trapped an adult male about a mile north of the campus. Its tail was barely an inch long and its wings were still in the process of molting. I put the bird in a darkened cage and took it by car to the campus, where I banded and released it in an area at that time unoccupied by Nuttalls; the area was later taken over by a pair and therefore must have been suitable. On August 31 I found the male back on the spot where I had trapped it. Three days later I retrapped it and found that the tail had not yet reached full length and the feathers of the pileum were still in sheaths.

On September 3 of the same year I tried an identical experiment with an adult female which was just starting to molt. I trapped and released her at the same points as I had the male, and nine days later found her back where I had trapped her. By this time she was molting heavily on the wings, breast, and belly. Her tail feathers had been renewed but were just beginning to grow out.

The significant point of these experiments is not that the birds returned to their breeding areas, but that they did so at a time when activity is normally reduced to the minimum and when the pairs into whose area they may have wandered would almost certainly have made no effort to drive them out.

Although the molt takes place while the gonads are regressing, there seems to be no rigid relation between stage of molt and testis volume. The testes of one male with much worn, but still unmolted, plumage had already regressed to 5.7 mm.[3], those of another with plumage in the same condition were still of breeding size (173 mm.[3]). The two extremes of testis size for four males just beginning the molt were 2.46 and 143.9 mm.[3] Two males which had almost completed the molt had testes of .94 and 1.29 mm.[3], respectively.

RETENTION OF TERRITORIES AND MATES

Permanent occupation of territory, through the year and from year to year, is the general rule, though I have found several exceptions.

Of 39 birds which I banded and watched for at least one breeding season, 17 bred in the same, or in a fraction of the same, area for two or more successive years; 2 were found dead in their areas before the end of the first sum-

mer; and 20 disappeared and were never seen again. There is every reason to believe that the latter also died. None was reported from any of the several banding stations or by any of the numerous ornithologists in Berkeley, in spite of the fact that the campus lies in the midst of a thickly populated area in which the only suitable places for Nuttall sparrows are parks and gardens, where a bird with colored bands would be likely to attract attention.

Of the 17 birds which survived more than one season, 5 were adults when banded and may have been present previously. Seven bred two years in the same area after being banded. Four shifted territories and mates in midsummer of one year but stayed in their new areas and bred there again the next spring. Two bred three years in the same area; 3, four years; and 1, probably five years. The latter (male I) was banded on May 20, 1932, by Dr. Seth B. Benson, whose notes indicate that the bird had partly immature plumage. The chances are extremely large, therefore, that it was hatched in 1931. On June 3, 1932, Dr. Benson saw the bird with its mate, feeding a family. On February 6, 1934, I found the male within a few yards of the spot where Dr. Benson had trapped him. His mate of 1932 had probably died, since a few days later I saw him with an unbanded, brown-headed bird with which he subsequently bred. The pair stayed in the same area until the summer of 1936, when both disappeared.

Of the 24 pairs followed, 8 remained unchanged for all or part of two or more breeding seasons. The rest were broken up. In 13 pairs, one or both disappeared during or following the first breeding season after they were banded. In 3 pairs, both members were known to have survived.

Of the 8 pairs in the first category, 2 remained unchanged for three years and 3 for two years, before one or both members disappeared. Two pairs, formed in May, 1937, were still intact a year later when I stopped watching. Another, also formed in May, 1937, remained unchanged until March, 1938, when both disappeared.

The shock of losing nestlings may have been responsible for two of the three desertions of one mate by the other. In 1937 females VIIIc and IVb had tried twice to raise broods. After the second failures both shifted to mateless males on adjacent territories and made one or more further unsuccessful attempts to breed. Female VIIIc stayed with her new mate and bred with him the following spring. Both mates of female IVb (males IV and VII) died before the next breeding season, and a new male, which settled in the area of male IV, bred with her. She nested in the same shrubbery she had used the previous spring.

The behavior of male IV, both before and after his mate deserted him, throws light on the nature of the bond between mates. It will be remembered that in 1937 he had two mates (females II and IVb), both of which he guarded from male VII, an unmated male which had, from February to June, tried repeatedly to enter his area. Now female IVb had built her first nest close to, and her second nest on, the southwestern boundary of her mate's territory, within five yards of a point where male VII spent most of his time. At 7 P.M. on May 15, the evening before she laid her first egg in her second nest, I found male VII foraging with her, about ten yards inside her mate's area. A few minutes later

male iv, who had been foraging with his other mate, female ii, a hundred yards away, detected the intruder, chased him out, sang loudly, and returned to female ii. Male vii flew back at once and lit in the same tree with female iv*b*. This set her off to trill and posture, whereupon her mate returned and again drove out male vii. Female iv*b* and her mate then flew east to the center of their area and copulated. This particular female, then, owing to her spatial isolation from her mate, the distraction of the latter's attention by a rival female, and her own proximity to male vii, had reached a condition which made either male acceptable. I do not mean to imply, however, that the females in general are indifferent to the individuality of the males with which they mate, for often this appears not to be true.

After June 2 her nestlings were destroyed, and I paid little attention to her for two weeks. On June 20 she was noticed with male vii about five yards on his side of the boundary. On June 23 I found her new nest, close to the boundary and near her last one, but definitely on male vii's side. It was now male vii that responded to her *ip* calls of protest by flying near the nest and also protesting. When she left to forage, he followed her about and urged her to return by flying near the nest and singing softly.

Male iv at this time showed no further interest in her, yet, five days after her young had hatched, I saw him carry food to her nest. On July 8 I saw him, while foraging with female ii, suddenly pick up a worm, fly across the boundary, enter the nest bush, and reappear without the worm. Neither male vii nor female iv*b* happened to be at hand. The next morning, however, when he again came trespassing with food, male vii drove him away twice. Male iv still clung to the worm and in a few minutes tried again, evidently succeeded in feeding the young, and flew back to his own ground. In this triangle two males became interested in one female. One male, her original mate, whether on account of the marginal location of the nest or the dividing and weakening of his defensive instinct by polygamy, was unable to retain possession. Yet his interest was still sufficiently persistent to extend through the lost female to her brood in another territory and doubtless by another mate.

Of the third pair which was broken up, the male became so interested in a neighboring widowed female that a bereft male was able to carry off his mate. In late May, 1937, male xxi acquired a widowed female, who had been established about 150 yards away across an unoccupied lawn. On May 27 I first saw him in her area, singing loudly. Once he approached her as if to copulate, then flew a little way off and sang again. With one exception I never saw him in his old territory again. Eight days later I did see him there, singing softly, but thereafter he restricted himself to the new area and mate. Meanwhile his previous mate, female xxi, had joined a bereft male on an adjacent territory. Both she and male xxi remained faithful to their new mates and bred with them again the next spring.

Perhaps male xxi would have been able to keep both females, had their areas been close enough together to patrol efficiently. The three other males that acquired second mates retained the first as well, but each time the combined areas covered about half as much ground as male xxi would have had to guard.

There is certainly a definite bond between mates other than common attachment to the same ground, for, when parts of the territory are pre-empted by immatures or mateless adults, the pair remain faithful. In 1935, for instance, the breeding area of male I covered about 1.7 acres. That winter eight to ten immatures and mateless adults settled there, and the next spring three of the males wrested about two-thirds of the area from male I. From January 9 to 26 the latter tried to drive them out but succeeded in holding for his mate and himself only the south central part of their former territory. All three of the invading males mated with immature females. Had mere attachment to the ground been the only bond the chances were at least three to one that female I would have mated with one of the new males.

TERRITORIAL BOUNDARIES

During fall and winter the territories are, with rare exceptions, undefended, although still observed, by the adults. With the coming of spring, first as the result of pursuits and fights and finally of patrol, the limits of each area become more and more sharply defined and are kept relatively rigid throughout incubation. They slacken with the fledging of the first brood, then tighten with the repetition of the nesting cycle. With the beginning of molt all defense and patrol cease, though the boundary sense must persist, since the pair stays within the area in spite of all temptations to leave it or natural tendencies to drift.

Even during incubation, when the boundaries are sharpest, they are never strictly linear in character, as Erickson (1938) describes them for the wren-tit. Except in 1936, when the number of pairs was the greatest in the five years, the territories on the campus never "abutted and interlocked" so that all available space was used. Between the areas of any two pairs there was usually a "no man's land," which might be definitely limited, like a road or a lawn, or might consist merely of a few yards of grass where either pair might forage without being driven out.

Nor were the boundaries rigid, even for a single season. With the fledging of the first brood, the male no longer devoted his entire attention to guarding the territory. Both parents would often wander with their young to one edge of the area, leaving the opposite side unwatched. Neighboring pairs with young frequently took advantage of the temporary absence of the owners to trespass on the edges of an unguarded territory. This is in general accord with the shading off and weakening of the instincts which we call "territorial" in the Nuttall sparrow as compared with those in the wren-tit, which Erickson has established as a standard for the positive extreme of territorial behavior.

THE CYCLE OF THE PUGET SOUND SPARROW IN RELATION TO THAT OF THE NUTTALL SPARROW

The behavior of the Puget Sound sparrow is similar in its broader aspects to that of the Nuttall sparrow, but with a wealth of minor variations. I shall use the cycle in the resident Berkeley population as a standard with which corresponding aspects of behavior in the northern migratory form will be compared.

THE BASE LEVEL : FALL AND WINTER

I know nothing of the rare individuals which have been reported to winter on the northern breeding grounds. The following account deals with the northern group or groups which migrate south in the fall to central California, probably from a far-northern section of the breeding range.

Arrival.—Unlike the Nuttalls, the adult Puget Sound sparrows leave their breeding areas in the fall and, with the young of the year, form large flocks, which persist for six or seven months. In late September and early October flocks of from twenty to fifty birds reach Berkeley, announcing their arrival by a chorus of song which is unmistakably distinct from that of the Berkeley Nuttalls.

Arrival dates are not identical for successive years, nor do all birds come on the same day in any one year. From 1934 to 1937 I saw the first Puget Sound sparrows on the campus on September 27, 30, 13, and 23, respectively. In 1935 a few birds came September 30, but it was not until October 5 that the first large flock arrived. In 1936 I heard a Puget Sound sparrow sing on September 13, and another observer heard one on the sixteenth, but I saw no large flocks until the twenty-sixth. In 1937 the period of arrival extended from September 23 to October 5.

Flocking.—In spite of the fact that one pair, at least, remated for two or more years on the same territory at Friday Harbor, I have detected no tendency to remain paired on the wintering grounds, no hint of such persistent mutual awareness as might reveal, within the winter flock, mates or nest mates of the past season. The flock is a homogeneous assemblage, without visible subdivision. It is more coherent than the smaller groups of immature Nuttalls. The latter are loose aggregates—individuals foraging on common ground, unified only by fright. The flocks of Puget Sound sparrows show a continuous simultaneity, a common responsiveness, producing true flock reactions.

Restriction to limited area.—Once on the wintering grounds the migrants show almost as strong a tendency to localization as do the residents. Year after year four flocks of Puget Sound sparrows have settled, each on a different area on the campus, and from the day of their arrival to that of their departure six months later have never left it but have foraged and roosted regularly at the same spots. Restriction to mutually exclusive areas is the rule, as has been proven at Palo Alto by the banding records of Price (1931). In February, 1928, by banding and by painting the tail feathers of Puget Sound sparrows on the Stanford campus, Price worked out the areas of three flocks and found almost complete mutual exclusiveness.

Voice.—The call notes of the Puget Sound sparrow are identical with those of the Nuttall sparrow. The song, however, is so different in pitch and rhythm that it constitutes one of the best criteria for distinguishing migrants from residents at Berkeley, though in other nearby localities, such as Carmel, the Nuttall song is more complex, and the criterion less reliable.

I have diagrammed (fig. 6) the predominant song patterns for the *pugetensis* population that winters in Berkeley. The first is the most common.

Toleration by the Nuttall sparrow.—The adult Nuttalls are perfectly tolerant of the Puget Sound sparrows for the whole winter season. Even in spring, when the resident males are ready to fight and drive out other male Nuttalls, they allow the *pugetensis* flocks to wander unmolested through their territories and may even forage peacefully in the midst of the flock, set off from the rest by distinctions which can hardly be based on physical appear-
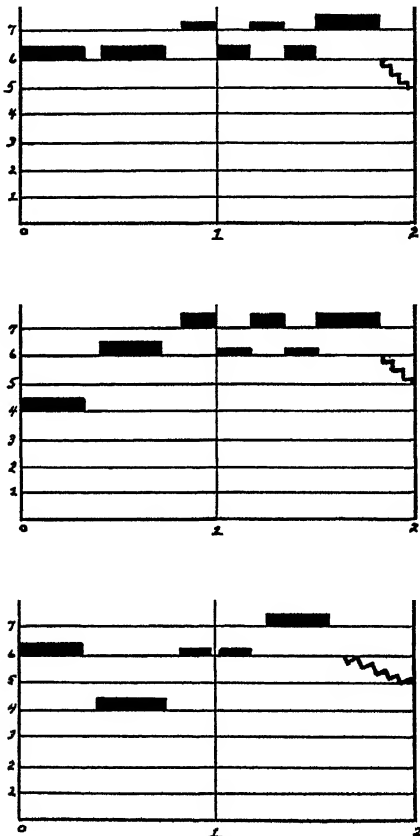
Fig. 6

Fig. 6. Diagrams of song patterns of Puget Sound sparrows wintering at Berkeley, California. Numbers on vertical scale indicate whole tones of pitch; numbers on horizontal scale indicate time in seconds. Thickness of bar indicates volume of sound.

ance. Differences in individual and flock behavior and in degree of aggressiveness undoubtedly account for the perfect cleavage between the groups. The larger flock of silent birds, obviously with no interest in the ground besides the food they are seeking, suggest no threat, rouse no jealousy. When a Nuttall landowner chances to hop or to fly straight at them, the Puget Sound sparrows always give ground, even to the extent of relinquishing a morsel of food too large to carry off. If a male Puget Sound sparrow should respond to the Nuttall's loud song by himself singing loudly, he would undoubtedly be driven out. This happened to a male Puget Sound sparrow which, probably owing to an injury, stayed on the campus in 1937 after the flocks had left for the

north. On the morning of April 25, some two to three weeks after all the other Puget Sound sparrows had departed, I found a lone bird singing every few seconds in an area not occupied by Nuttalls. The pattern of the song was unmistakably that of a Puget Sound sparrow, but the bird sang as loudly as any male Nuttall, as his flock mates had probably begun to do a thousand miles to the north.

I heard the bird singing in the same place several times during the ensuing week and on May 9 watched him try to invade the territory of a neighboring pair of Nuttalls (xxi). At 9:30 in the morning I found him perched within a few feet of male xxi on the boundary of the latter's area. Male xxi trilled vigorously, pursued the intruder a few yards, then disappeared, whereupon the Puget Sound sparrow sang loudly several times. In a few moments male xxi returned and twice more pursued the stranger, which flew slowly and a little unevenly, as if he had difficulty keeping his balance. At nine the next morning I found him at the same spot, singing incessantly, and saw male xxi chase him again. The evening of May 11 I trapped him at this same spot but could find no injury. I found he had retained the abundant fat characteristic of Puget Sound sparrows on the verge of migration, but that, as might be expected from his insistent singing, his testes had reached almost full breeding size (103 mm.'), a volume over twenty-five times as great as the average for Puget Sound sparrows previous to departure.

THE RISING TIDE: SONG, MIGRATION, TERRITORY, AND PAIRING

Behavior before departure.—Up to the day of departure, the behavior of the wintering flocks suffers no radical change except for the increased frequency of song, beginning some four weeks before migration. At first one or two birds may break into occasional song, from the center of the flock or from some point apart, only to re-enter the group at once. As departure becomes imminent, the number of singers increases until, by a week or so before migration, the whole flock may fly together to a tree and burst into song.

The beginning of frequent singing, though it foreshadows a similar series of events, is not strictly comparable to the spring increase in song of the Nuttall sparrows. In the latter, the beginning of loud and frequent singing is largely an act of hostility, a warning to rivals to keep their distance, and is accompanied from the first by pursuits and fights. The attitude of the singer is one of defiance. He perches conspicuously, and raises his crown as he sings. This evokes a like response from other males and stimulates the female to trill and posture.

In the wintering Puget Sound sparrow singing has not yet become an act of defiance and provokes no hostile response from others of the same sex, nor indeed any response unless perhaps further group singing. Neither chasing nor fighting, other than occasional momentary disputes over food, occurs on the wintering grounds. There is no stimulation of trilling and posturing in the female. Neither territorial jealousy nor sexual excitement have yet come to the surface. The coherence of the flock is maintained up to the moment of departure.

Departure.—In so far as behavior is concerned, the gradual swelling of the chorus of song is the only change I can detect which foreshadows the departure of *pugetensis* in late March and early April. Since not all birds leave on the same day, only careful counts can reveal the first to go. Close watching and regular trapping in the same spots, day by day, reveal a gradual reduction over a period of at least two weeks. Once the numbers begin to dwindle, they continue to do so until at last only three or four birds remain where a fortnight before there may have been fifty. There is never an increase or such stability of numbers as would result if migrants from the south filtered in to replace the departures. Specimens collected from the same spot during the decrease turned out to be individuals which had not yet reached the maximum testis size for birds on the wintering grounds and which had not yet completed the molt or laid on the maximum amount of fat. As will be discussed more fully later, variations in departure time for members of one flock undoubtedly reflect individual differences in physiological readiness for migration. The annual dates are discussed in another section in connection with the gonad cycle.

Arrival on the breeding grounds.—For reasons to be discussed in a later section, I believe that the longest spring migration is accomplished in not more than two weeks. I know nothing of behavior during this period. The following account is based on observations of birds in 1936 from the moment of their arrival on the breeding grounds at Friday Harbor, Washington.

On April 7, when I myself arrived at that point, I spent the day searching several miles of white-crown country which was soon to be heavily populated. I found, however, only rare individuals, of both sexes, already arrived or conceivably—in very rare instances—present after wintering over.

The great influx of breeding birds occurred between the evening of April 9 and the next morning. By nine in the morning of April 10 I found almost every piece of suitable land, which only the day before had been empty and silent, occupied by a male, perched conspicuously and singing with full volume every few seconds. Close to him I often saw another, silent, bird, the female.

The shift from the complete, unassorted gregariousness of the wintering grounds to paired isolation must have taken place either during migration or immediately upon arrival, for there were no flocks or fragments of flocks. Of the scores of birds I saw and heard singing that first morning, all were isolated, some in pairs, some apparently alone, though it was hard to be sure of the absence of the silent and inconspicuous females, especially in my preoccupation with collecting, as well as watching, the males.

I have some evidence to indicate that on the day of arrival the birds go directly to the areas where they subsequently breed and that they return to the same spot in successive years. Mrs. Forrest Fuller, a resident of Friday Harbor, had previously told me of a pair of Puget Sound sparrows which had nested the year before in a chamaecyparis hedge in front of her house. On April 10, 1936, Mrs. Fuller saw for the first time that year a pair of Puget Sound sparrows perched on the same hedge. One sang loudly, the other was silent. I watched this pair from that day on until April 14, when I color-

banded them. The female subsequently built her first and second nests in the hedge. The following year the same pair returned and nested in the same shrubbery.

Although by far the greater number of birds came in a body on April 10, not all came on that day. I noticed a second, lesser, influx on April 14. Thereafter, unless with the exception of one pair which, on April 20, occupied a previously empty site, there was no further increase in numbers on the area that I was watching closely.

Song.—Loud, persistent singing, now entirely comparable in force and significance to the spring song of the Nuttalls, continued from the morning of arrival to about April 18, three days before I first saw copulation. Then it subsided, but was resumed about two weeks later, at the start of incubation. If we assume that the period of loud, purposeful singing began upon arrival, it lasted only eight days. Such an assumption receives some support from the evident inconspicuousness of transient birds at all stations. Eight days is less than one-third of the corresponding period of song in the Nuttall sparrows of Berkeley. The ensuing interval of silence was also about one-third as long as the average for the Nuttalls (14 days as opposed to 52 days). Furthermore, the relation of singing to other elements of behavior and to the stages of testis development was different. In *pugetensis* singing continued until a few days before copulation. In *nuttalli* singing of mated males ceased about six weeks before copulation. In *pugetensis* the period of loud singing coincided with the increase in testis volume from about 55 mm.³ to full breeding size (100 mm.³ or more). In *nuttalli* the period coincided with the segment of testis development from about 4 mm.³ to 20 mm.³

I have diagrammed in figure 7 the predominant song patterns for the Friday Harbor population.

Chasing and fighting.—I saw no pursuits or fights on the day of arrival, but might have missed them since I spent most of the day collecting rather than watching. From the next day on, however, both chasing and fighting were common and continued unabated until the beginning of incubation, some three weeks later. It will be remembered that in *nuttalli* most of the pursuits and fights stop with the subsidence of song and general settlement of territorial problems some seven weeks before incubation begins.

Furthermore, in the Puget Sound sparrows, conflicts between neighboring pairs took place at so many widely separated points that it was impossible to establish a border line between any two areas. In fact, from the day of arrival until the start of incubation, territorial boundaries were so fluid as scarcely to deserve the name. To be sure, each pair had a headquarters, a clump of shrubs or trees where they spent much of their time. Frequently, however, they made long excursions, even as far as, or beyond, the headquarters of a neighboring pair and were almost as frequently driven out by the owners.

Both sexes seemed more excitable and restless than Nuttalls in the corresponding stage. The males were more prone to trill and posture, the females to take part in the pursuit of an intruder. Both made long flights back and forth between opposite parts of the area. The whole scene was one of confusion,

of unsettledness, in sharp contrast to the orderly and law-abiding behavior of the Nuttalls on their mutually exclusive areas during the seven weeks before the start of incubation.

Eventually, however, the same result was achieved. By the first day of incubation the fighting subsided and the pairs settled down to a routine identical with that of the Nuttalls. The female sat on the eggs, and the male sang all day and patrolled his territory. In about three weeks, a period slightly shorter than that required by the Nuttalls for the same process, territorial establishment was finished. The battle for land had been more brief, but also much more fierce.
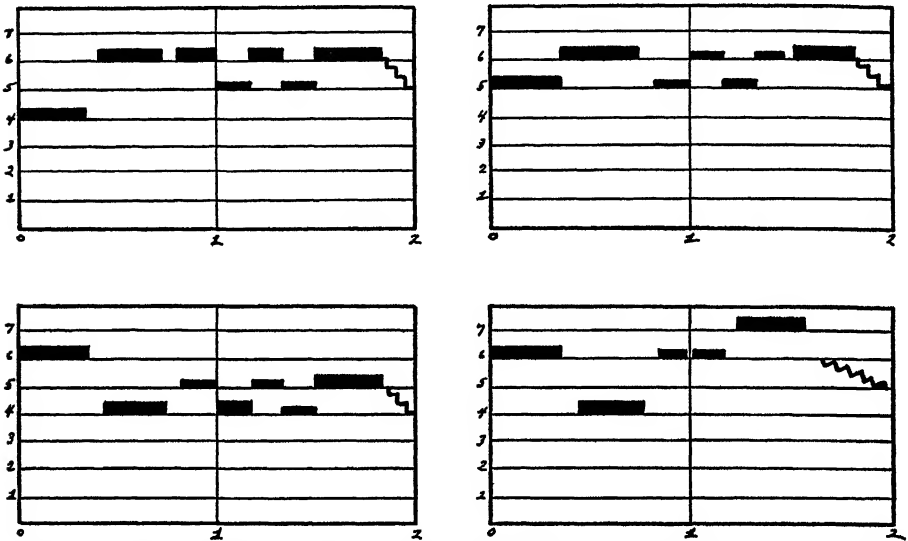
Fig. 7. Diagrams of song patterns of Puget Sound sparrows at Friday Harbor, Washington. Numbers on vertical scale indicate whole tones of pitch; numbers on horizontal scale indicate time in seconds. Thickness of bar indicates volume of sound.

The relative disorder among the migrants during the "shake-down" period is not unnatural and may represent merely the result of circumstances rather than an intrinsic variation in habit or temperament. The migrants must establish themselves on ground unseen for seven months and perhaps wholly unfamiliar to some fraction of the adult birds. The first-year birds must seek and seize at once what the young Nuttalls drift into or seek at leisure. The sudden change from a gregarious to an isolated habit perhaps creates a deeper psychological disturbance and contributes to the violence of the process of spatial arrangement.

Trilling and posturing.—I first saw a female trill and posture on April 12, two days after the main arrival. From this time on, trilling and posturing increased in frequency and vigor until April 21–27 when copulation began. Then, as with the Nuttalls, both ceased temporarily, to be resumed in lesser degree with the repetition of the nesting cycle.

In *pugetensis*, then, the period of trilling and posturing was compressed to three weeks, or, if it started during migration, to not more than five weeks,

as opposed to from nine to eleven weeks in *nuttalli*. At least as far as behavior on the breeding grounds was concerned, the long period of sporadic trilling and posturing, characteristic of the cycle in *nuttalli*, was omitted. Like the Nuttalls, the female Puget Sound sparrow often trilled and postured just after the singing of a male or during a pursuit or fight in which her mate was involved.

I have already spoken of the frequency with which male Puget Sound sparrows trilled and postured. This was common at Friday Harbor, whereas from five seasons' watching of Nuttalls I have only fourteen records. Although this reaction occurred under a variety of circumstances, its connection with territorial jealousy was more obvious than in the Nuttall.

In both migratory and nonmigratory populations, then, territorial jealousy and sexual excitement, as well as other more incidental emotions, are manifested in identical ways: by loud singing, pursuits and fights, trilling and posturing. The duration of the prevalence of these elements, however, and their relation in time to other elements of behavior and to the gonad cycle, differ radically.

In *pugetensis,* segregation and territory establishment take place in the three weeks immediately prior to, and including, copulation and egg laying, and during and immediately following the latter half of the increase in testis volume. In *nuttalli* the same process is finished seven weeks before copulation, before the testis has reached one-fifth of its maximum size.

REPRODUCTION

Behavior of both sexes during nest building, copulation, egg laying, incubation, and care of the nestlings was identical with that already described for the Nuttalls and will not be reviewed here. The time spent in building the nest and incubating the eggs, as well as that spent by the young in the nest, was likewise identical. Nonetheless, deep-seated physiological differences exist, chief of which are the larger size of clutch in the northern populations, the earlier independence of the fledglings, and the compression of the interval between completion of the nest and laying of the first egg, and between the fledging of one brood and the laying of the next clutch.

Nest.—By April 17–23, only one to two weeks after the arrival of the birds on the breeding grounds, nest building was in progress. Since the trees and shrubs were not fully leafed, it was possible to see many of the nests in process of construction from a distance of several yards. The growth of the foliage was so rapid, however, that before the first eggs were laid, the nests were well concealed.

The Puget Sound sparrows showed even greater catholicity of taste than the Nuttalls in the matter of nest sites. Many kinds of native and introduced trees and shrubs were used, and 14 of the 45 nests which I found were built on the ground, in masses of dense scrubby salal (*Gaultheria shallon* Pursh) or in dead bracken (*Pteris aquilina* L. var. *lanuginosa* Bong.) or grass. None of my 44 Berkeley Nuttalls' nests nor any of the 17 which Grinnell and Linsdale (1936) found at Point Lobos was on the ground. Mr. H. W. Carriger

(MS) states, however, that he has occasionally found Nuttalls' nests on the ground although "nests are usually from six inches to three feet from the ground."

Perhaps the greater thickness of ground cover at Friday Harbor as compared with central California accounts for this difference; yet all the territories of Puget Sound sparrows with ground nests contained thick shrubbery apparently suitable for nest sites. In fact, four females which built one nest on the ground were known to build others in the shrubs. One female combined both extremes by putting her first nest on the ground and her second over thirty feet above the ground. The average height of thirty-one nests was 3.2 feet, slightly lower than the average for *nuttalli* (3.5 feet).

One nest which I found the day the female began to build was finished in seven or eight days, about the same time required by female Nuttalls to build a nest.

Eggs.—From one to four days after the nest was completed the first egg was laid. The interval averaged between 2.4 and 2.9 days for seven records. This interval is slightly shorter than in the Nuttall sparrows, which average 3.6 days for twelve records.

With respect to the interval between copulation and first eggs, I saw one pair copulate nine or ten days before the first egg was laid and another pair, three days before.

The size of the clutch averaged larger in the Puget Sound sparrows than in the Nuttalls. The number of eggs varied from 3 to 5. The average of 44 nests from the Seattle–Friday Harbor–Victoria region was 4.09, as opposed to 3.25 for 147 nests of the Nuttall sparrow. In terms of percentages, in the Puget Sound sparrow 11.4 per cent of the clutches had three eggs, 68.1 per cent had four, and 20.5 per cent had five. In the Nuttalls 4.8 per cent had only two eggs, 66.0 per cent had three, 28.5 per cent had four, and .7 per cent (one set only) had five. This provides another example of the well-known principle that in the northern hemisphere the farther north the breeding population of a given species, the greater the number of eggs per clutch.

As in the Nuttall sparrows, the second clutch averages larger than the first. Of 22 first clutches, 3 had three eggs, 19 had four eggs. The average was 3.8. Of 7 second clutches, 4 had four eggs and 3 had five eggs. The average was 4.4. A single third clutch had five eggs.

Incubation.—The beginning of incubation in relation to egg laying showed about the same variation as in the Nuttall sparrow. Of four female Puget Sound sparrows with clutches of four eggs each, three had started to incubate on the day the third egg was laid, and one probably on the day the fourth was laid. One female with three eggs started on the day the third was laid.

The length of the incubation period was the same as in *nuttalli*. In four sets the eggs hatched 12 days after the day incubation started. In one clutch the interval was 11½ days for the first egg to hatch, but 12 days for the other two eggs.

Hatching.—The eggs of any one set show approximately the same variability in hatching time as do those of the Nuttall. The eggs of the three sets which

I marked did not hatch in the order laid. One set of three hatched in the order 2, 1, 3, another in the order 3, 2, 1. A set of four hatched in the order 2, 1, 3, 4.

Young.—The development of the Puget Sound sparrow nestlings corresponded closely, in both behavior and morphology, to that of the Nuttalls. Weights in two broods for the first six days after hatching varied within the same limits as those of Nuttall nestlings of the same age.

The average age at fledging was also identical. Of eight broods of known age seven left the nest when ten days old, one when eight days old.

The behavior of the parents up to the time the young left the nest was identical with that of Nuttalls. For about the first week after the young were fledged the female alternated between feeding them and building the second nest. Thereafter the male took over all care of the fledglings. It will be remembered that in the Nuttalls, on the other hand, the work of feeding was shared by both parents for about three weeks. This would have been impossible in the Puget Sound sparrows, since, on an average, eleven days after one brood had been fledged the female had already begun to incubate the second clutch of eggs. From then on, the males performed the duties of feeding the fledglings and guarding the territory and the second nest. They often made short excursions with their young outside the territory, but never for more than a few minutes at a time. Once I found three males from contiguous areas foraging with their young in the same 50-yard-square raspberry patch. None appeared to resent the presence of the others.

As the time for the hatching of the second brood drew near, the males spent more and more time near the nest and less in feeding and watching the fledglings. It may have been owing to this neglect that the young birds left their parents' territory at an earlier age than did the young Nuttalls. Out of seven broods of fledgling Puget Sound sparrows which I watched almost daily, the oldest to be fed by the male was 27 days old. One young bird was found alone, across the border from its parents' territory, when only 25 days old. Two broods of young from neighboring areas were seen foraging independently outside their parents' territories when only 26 and 28 days old, respectively. The following day I came upon a small flock made up of these two broods and another which was 31 days old, a circumstance which may offer some evidence on the composition of the migratory and wintering flocks. It will be remembered that young Nuttalls may stay in their parents' territories, and may even be fed by the male, until they are 35 days old.

Second and third broods.—Owing to the compression of several phases of the cycle, particularly of the interval between broods, the Puget Sound sparrows, although they began to breed over a month and a half later than the Nuttalls, had time to raise three broods before the regression of the testes in late July. Unfortunately, I was obliged to leave Friday Harbor before the fledging of the third brood could be recorded. Two females which had fledged two broods each were sitting on their third clutches at the time of my departure. All but two of the remaining eleven pairs of the group I watched would have had ample time for a third brood before gonad regression, as recorded from other stations of like latitude. The general average of success with the

broods was not high. Before I left, only three out of thirteen pairs raised two broods successfully, whereas the remaining ten all raised one and made one or more further unsuccessful attempts.

From two to four days after the first brood was fledged, the six female Puget Sound sparrows which I followed started work on their second nests. I saw two pairs copulate two and three days after their young had left the nest. The first egg of the second clutch was laid from 6 to 15 days after the fledging of the first brood (an average of 8.9 days for five records). In the Nuttalls the corresponding interval was over twice as long (from 14 to 29 days, or an average of 20 days, for six records).

As in the Nuttalls, the second nesting cycle followed the same pattern as the first, except that trilling and posturing was much less frequent. During the interval between first and second broods I followed closely the behavior of female x, already mentioned as the bird which nested for at least two years in the same chamaecyparis hedge. On May 25 at ten in the morning the two nestlings which had survived from her first brood hopped out of the nest and perched near by in the same hedge. The next morning I watched her for over an hour and saw her feed the young several times. Once she carried an inch-long straw to the hedge and entered, but without the *eep* note usually associated with nest building. I searched the place but found no sign of a nest.

The next day I saw her pick up a twig while she foraged, only to drop it without carrying it to the hedge. She must have started to build later that day, however; the next morning (May 28) I saw her disappear with material into the hedge a few feet to one side of the first nest site. There I subsequently found a new nest with the walls partly formed.

That the alternate feeding and building may result in confusion was illustrated the same morning. Between half-past eight and half-past nine she made seven trips to the hedge to feed the fledglings, then stayed away for half an hour. She returned at ten, carrying straws in her beak, flew to the abandoned nest, hesitated a little, flew to the hedge where a nestling was perched, and emerged without the straw. I sought out the fledgling, which was crying for food, and found she had laid the straws at its feet!

About fifteen minutes later, female x brought food to the fledgling, then perched on top of the hedge; whereupon her mate approached and copulated with her three times. She neither trilled nor fluttered her wings before the male mounted her but merely raised her tail high as he fluttered above. Five minutes later she again flew to the hedge with straws in her beak and this time went straight to the new site. When I looked at the nest that evening, its walls were complete, and a few pine needles and a little fine grass were heaped in the cup.

During the next two days she added a little more of the latter materials and wove them into a compact lining. On May 31, just six days after the first brood had left the nest and three days after I had seen the pair copulate, the first egg was laid. At 10:45 that morning I saw female x make another trip to the nest, presumably with more material for the lining, since I found some hairs which had not been in the lining before. Here, therefore, nest building and

egg laying overlapped, whereas, in the case of the female Nuttalls which I watched during the corresponding period, intervals of two and three days elapsed between the completion of the second nest and the laying of the first egg.

THE EBB: FLOCKING, MOLT, MIGRATION

My observation of the Puget Sound sparrows at Friday Harbor ended on July 12, 1936. I know nothing of their behavior during the remainder of their stay on the breeding grounds. For the same year, however, I have, through the kindness of Mr. Patrick Martin, records of the approximate time of molt and of the fall migration for the breeding birds at Victoria, B. C., close at hand and similar in character of country. Of five adults taken by Mr. Martin August 4 to 13, all were much worn and only one had begun to molt. Three birds taken September 1 had complete new plumage except for a few feathers of the head still ensheathed and rectrices not quite fully grown. A bird taken September 14 had completely fresh plumage with all feathers fully grown out.

Mr. Martin (MS) says that by August 6 the birds were "collecting in flocks of three to four family groups." The last day on which he saw a large flock was September 14. That year the large flocks reached Berkeley on September 26. If we assume that the birds from this region migrate as far as Berkeley— and we have a record of one bird which made this exact flight in the reverse direction (Clabaugh, 1929)—then the flight south took about 12 days. Since the birds probably do not begin to migrate until they have nearly, if not fully, completed the molt, and since the specimens taken September 1 had not yet finished, it is probable that the earliest to leave Victoria would not have departed until the end of the first week in September. Hence the longest time spent in migration would have been three weeks.

SUMMARY AND DISCUSSION

The most striking fact which emerges from this mass of detail is that the birds which pay heavily in time and energy for the doubtful privilege of nesting in the relatively inclement, capricious, and short-seasoned latitudes of the Canadian border compress the active part of their reproductive cycle into less than two-thirds the time consumed by the populations of central California. In 1936 the birds at Friday Harbor segregated into pairs, established territories, and fledged three broods in less than four months. In the four years from 1935 to 1938 inclusive, the Berkeley birds consumed from 6 to 6½ months (an average of 6.3 months) to achieve the same fraction of the cycle.

I have prepared a composite diagram (fig. 14) of the cycle in *nuttalli* and *pugetensis* for 1936 to bring out the contrast in length of the reproductive periods. The graph of behavior and testis development in *pugetensis* is composite, that is, it represents observations and specimens from three localities, though two are of similar latitude and character: from January to April at Berkeley, from April to July at Friday Harbor, for August and September at Victoria, and from October to December again at Berkeley. Also the dates for the first eggs of the second and third broods for Berkeley *nuttalli* had to be calculated from the averages of the four other years, because I had to follow *pugetensis* to Friday Harbor before the time of the second brood in Berkeley.

The compression of the cycle of *pugetensis* results from the omission of one, and the shortening of three other, more or less sharply delimited phases. In *pugetensis,* territorial establishment requires about 3 weeks and is not complete until the first day of incubation. In *nuttalli,* territorial establishment also takes about 3 weeks, but is begun much earlier, so that it is finished some 6½ to 8½ weeks before the first day of incubation. The ensuing period of 46 to 59 days, between the time of decrease or disappearance of chasing and fighting and the first day of incubation, is entirely omitted in *pugetensis.* The three phases which are shortened are: first, the period of temporary abeyance of song (14 days in *pugetensis* as opposed to 46 to 59 days in *nuttalli,* depending upon the year); second, the interval between completion of the first nest and laying of the first egg (an average of 2.6 days in *pugetensis* as opposed to 3.6 days in *nuttalli*); and third, the interval between fledging of one brood and laying of the first egg for the next (an average of 8.9 days in *pugetensis* in contrast to 20 days in *nuttalli*).

I have mentioned the possibility of the compression of two other phases: loud singing at the first of the cycle and the interval between completion of the second nest and laying of the first egg of the second clutch. Concerning the first possibility, if loud singing begins with arrival on the breeding grounds, then the period lasts only eight days as opposed to an average of twenty-six days in *nuttalli.* It may, however, begin during migration. Concerning the second possibility, data on more pairs are needed before a shorter interval for *pugetensis* can be proved.

It is significant that the phases which showed the greatest variability between the two races are those which showed the greatest individual variation in the Berkeley Nuttalls. For the latter the period of the temporary abeyance of song may last as long as 59 days or may be omitted entirely if the male fails to get a mate before incubation begins in the population as a whole. The interval between completion of the nest and laying of the first egg varied from one to seven days in *nuttalli;* that between the fledging of one brood and the laying of the first egg of the next, from fourteen to twenty-nine days.

As a corollary, those phases the lengths of which averaged the same in both populations showed the least individual variation in *nuttalli.* The time spent in building the first nest (seven days for one Puget Sound female) varied between 7 and 8 or 9 days for three female Nuttalls. The two extremes in *nuttalli* for length of incubation were 12 and 14 days; those for age of young at fledging, 8 and 11 days.

Although I have no intention, in the present section, of going seriously into the matter of the application of these differences to the problem of geographic distribution, it is perhaps worth indicating a line of thought based upon them.

Under present conditions the rapid development on the breeding grounds and the compression of the breeding season of *pugetensis* seems of little value. At the end of the season there is yet warm weather to spare. Nonetheless it is reasonably certain that in the latitude of Puget Sound and the Gulf of Georgia, at the end of the last episode of the Pleistocene, far more severe con-

ditions prevailed. It is highly probable that migration and the compression of the cycle are the result of thousands of generations of crowding upon climatic conditions which represented the limit of tolerance of these birds—conditions which have now passed northward where the birds cannot follow, because the transformation of the coast and its vegetation practically eliminates their habitat. The variability of the migratory habit, with its failure to function in the odd birds which winter on the northern breeding grounds, probably indicates not an incompletely acquired habit, but rather the decline of a habit which is now without value or of greatly reduced value.

Such a situation probably obtains with respect to other birds of the northern and middle latitudes of the United States. Nice's (1937) analysis of the migratory habit in the Mississippi song sparrow is pertinent here.

THE GONAD CYCLE OF THE MALE NUTTALL SPARROW

INTRODUCTION

My material for the investigation of the gonad cycle consisted of large series of Nuttall sparrows collected at Berkeley. Most were brought into the laboratory alive and, within ten to fifteen minutes after death, were skinned and put into Bouin's solution.

Before sectioning the testes, I measured the longest and shortest diameters. Usually both testes were almost identical in size. As other workers on various species of passerine birds have found, when there was a difference, the left testis was nearly always the larger. I measured the larger testis of each bird with calipers and computed its volume in cubic millimeters, using the formula for the volume of an ellipsoid, $V=\frac{4}{3}\pi ab^2$, where $a=\frac{1}{2}$ the longest diameter and $b=\frac{1}{2}$ the shortest diameter at the widest part of the testis.

I sectioned one hundred and fifty testes, one hundred of which were less than twelve cubic millimeters in volume. The other fifty were taken from each of six larger-size groups, including breeding size. The small diameters of the hundred small testes were checked by measuring the diameters of the largest cross section with an ocular micrometer calibrated in millimeters. Whenever the two methods disagreed, I took the ocular micrometer reading and recalculated the volume. A mistake of comparable scope in the larger testes made little difference, so the hand measurements were allowed to stand. Cross sections were made of a thickness of 10μ. When the testis was too large to be mounted on a single 76×25-mm. slide, the center only was sectioned.

Most testes were weighed before sectioning. Since the testes had to be kept continually moist, this task proved time consuming, and not all of the smaller ones were weighed. A bottle containing a little 70-per cent alcohol was weighed first. The testis, also in 70-per cent alcohol, was taken out of its container, laid for a moment on a cork to take off the excess alcohol, and put in the weighing bottle, which was then weighed again. Some discrepancies between size and weight were found, perhaps attributable to the deficiencies of the method. The weights ranged from a minimum of less than 1 mgm. to a maximum of 204 mgm. Average testis volumes and weights are shown in table 5.

Weight increases of similar magnitude have been noted in many species (Bergtold, 1926; Rowan, 1929; Kirschbaum and Ringoen, 1936; and others).

Examinations of the sections, stained with Harris' haematoxylin and eosin, showed that, for testes above 2 mm.^{3}, size is a reliable criterion of histological condition but cannot be trusted for smaller specimens, which may belong to any one of the first three histologic stages described below.

Two kinds of graphs were made to show the annual recrudescence and regression of the testes. Five large graphs (figs. 8–12), one for each year, were made with a scale sufficiently small to include the larger testes. This required too small a scale to show those below 4 mm.^{3}, so smaller graphs (figs. 15–19)

TABLE 5

NUTTALL SPARROW TESTES: AVERAGE VOLUME AND WEIGHT

Number	Average Volume (mm.^{3})	Average Weight (mgm.)
5............................	0.52	<1.0
5............................	1.29	1.0
9............................	2.96	2.9
1............................	5.49	5.5
3.	9.93	12.0
2..........................	23.24	25.5
1..	38.99	47.0
2.....	63.25	85.5
3..........................	123.36	136.3
1..........................	140.49	204.0

were made to show the smallest volumes. Since, for testes below 2 mm.^{3} size did not correlate precisely with histologic condition, I indicated the successive histologic stages with different symbols to make the annual series comparable. From 1935 to 1937, all testes below 2 mm.^{3}, and most between 2 mm.^{3} and 4 mm.^{3}, were sectioned.

HISTOLOGIC STAGES IN THE MALE

The following description of the histologic stages is for the Nuttall sparrow. The gonad cycle of the Puget Sound sparrow follows essentially the same course but differs in time of appearance of the stages and in rate of development. The differences will be discussed later.

The testes of adult Nuttalls reach an inactive state (volume .25–.53 mm.^{3}) by early or mid-October and remain in this stage during early November at least, and probably during the whole of November. From middle or late December on, the gonads show the earliest histological changes. This is evident in several testes which are no larger than inactive October–November specimens. However, table 7 shows some evidence of an almost imperceptible increase in volume running throughout the winter. Special work is needed to decide this point, with delicate apparatus and more abundant material. In any event, the ensuing rate of increase is variable, with a sharp rise prior to breeding, as will be discussed below. From the twenty-two testes with an average volume of

137.92 mm.³ collected at scattered dates from March to July during four years, it seems safe to assume that the testes remain at this high level throughout the breeding period, until middle or late July when regression begins. Decrease in size is very rapid at first, then slows down, and continues during September and at least part of October until the inactive level is reached. Thus the curve of sexual regression, if reversed, is very like that of progression, with rapid change close to breeding time shading off to a common period of inactivity or to a period when the changes are too small and too slow to be perceived. The opposite sigmoid curves which precede and follow midwinter are similar, though the former is somewhat steeper.

Volume changes of a similar order of magnitude have been described for other passerine birds (Loisel, 1900, 1901, 1902; Kirschbaum and Ringoen, 1936, *Passer domesticus;* Watson, 1919, *Ligurinus chloris;* Rowan, 1929, *Junco hyemalis;* and Bissonnette, 1930, *Sturnus vulgaris*). These workers likewise emphasize a similar character of curve with its late sharp rise, which in most of these other species, however, occurs a month or more later. This is extremely important in considering possible correlations with the physical conditions of the environment, which are changing far more rapidly in the spring than in the winter.

I shall describe the histologic stages only briefly, since they have already been analyzed in detail for the other passerine birds just mentioned. The present object is not to study the histology per se but to obtain fixed points for the study of the successive annual cycles.

STAGES 1–7, INACTIVE TO BREEDING CONDITION

Stage 1: Inactive condition—

Designated by triangle in graphs (figs. 15–19); volume range = .25–.53 mm.³; average volume (7 testes) = .39 mm.³; photomicrographs, plate 5.

The size of the seminiferous tubules, as well as of the whole testis, is at a minimum. Each tubule contains one or two rows of small spermatogonia ("spermatogonies de premier ordre" of Loisel), which lie against the limiting membrane of connective tissue. There are in addition large spermatogonia ("spermatogonies de deuxième ordre" of Loisel) wedged between the small ones. The rest of the tubule contains clear cytoplasm and is without a lumen. Intertubular cells, referred to by Rowan and Bissonnette as "connective-tissue cells," form about six to seven rows between adjoining tubules. It is open to question whether these cells are of the true connective-tissue type or are interstitial cells in the nonfunctional state. No interstitial cells in the functional state are present. The tunica albuginea is thick and spongy. This corresponds roughly to the inactive testes of other passerine birds as described by the authors just cited.

Stage 2: First change from inactive condition—

Designated by horizontal rectangle in graphs; volume range = .50 mm.³–1.09 mm.³; average volume (14 testes) = .82 mm.³; photomicrographs, plate 6.

A few cells resembling functional interstitial cells, with a large spherical nucleus and a single nucleolus, are scattered irregularly among the cells of the

nonfunctional type, which still form six to seven rows between the tubules. Both types of spermatogonia may be more numerous than in the winter condition, but their arrangement within the tubule is virtually the same. This stage corresponds roughly to "recrudescence" as described by Rowan for the slate-colored juncos.

Stage 3: Marked increase in germinal elements and interstitial cells—
Designated by vertical rectangle in graphs; volume range $= .78$ mm.^{3}–1.83 mm.^{3}; average volume (10 testes) $= 1.42$ mm.^{3}; photomicrographs, plate 7.

Within the tubules there is a marked increase in numbers of cells, many of which are moving toward the center, and some of which may have reached it. Some of the larger, more central cells are probably primary spermatocytes. There is still no lumen. Some large spermatogonia are dividing; others are degenerating. Several of the latter, which are vacuolated and have opaque nuclei, may usually be seen in any one section. Functional interstitial cells are common—in some places filling the entire triangles between adjoining tubules. There is a marked reduction in the "connective-tissue" (nonfunctional interstitial) cells, which now form only two or three rows. The tunica albuginea is becoming thinner and slightly fibrous.

Stage 4: Appearance of primary spermatocytes in synapsis—
Designated by square in graphs; volume range $= 1.73$ mm.^{3}–5.18 mm.^{3}; average volume $= 3.02$ mm.^{3}; photomicrographs, plates 8 and 9.

By this time the tubules have become noticeably larger; they continue to enlarge up to breeding time. In most of the tubules of any one cross section are one or more primary spermatocytes in that stage of synapsis in which the chromatin is pressed to one side of the nucleus. A lumen is probably present but so filled with desquamating cells that no space is visible. Functional interstitial cells now fill all the triangles between the tubules and may even lie along the sides of the tubules between the "connective-tissue" cells, which are reduced to two rows. The tunica albuginea is thinner and more fibrous. This corresponds to junco testes of nearly 2 mm. diameter described by Rowan, and, at least as far as the cells within the tubules are concerned, to starling testes 11.07 mm.^{3} in volume described by Bissonnette and Chapnick (1930).

Stage 5: Predominance of primary spermatocytes in synapsis—
Designated by circle in graphs; volume range $= 5.5$ mm.^{3}–13.0 mm.^{3}; average volume (12 testes)$=8.13$ mm.^{3}; photomicrographs, plate 10.

The entire space of the markedly enlarged tubule not occupied by spermatogonia is taken up by primary spermatocytes in synapsis, of which there may be four rows. At the center, which may show the beginning of a definite lumen, there are sometimes a few secondary spermatocytes, although these are rarely seen until spermatids are also present since the former divide almost immediately to give rise to the latter. Interstitial cells are fewer in relation to the total area of the section, but it would be necessary to make elaborate counts to ascertain whether or not they are actually fewer. The tunica albuginea is very thin and fibrous. This corresponds roughly to starling testes 11.83 mm.^{3} in volume.

Stage 6: Spermatids present—

Volume range=19.7 mm.³–52.3 mm.³; average volume (6 testes)=34.10 mm.³; photomicrographs, plates 11 and 12.

Spermatids, cells with very small circular nuclei, may be seen bordering the lumen of the tubule. A few spermatids, in various stages of metamorphosis, are moving away from the lumen. A few mature sperms have already formed and are grouped in bundles of three to five, their heads pointing away from the lumen. This corresponds roughly to junco testes 3.5 mm. in diameter and to starling testes 91.66 mm.³ in volume.

TABLE 6

FIRST COPULATION AND TESTIS SIZE

Year	Dates of First Copulations	Median Dates of First Copulations	Gonad Volume (mm.³)	
1935.....................	March 19 (2 pairs) April 4 April 11	March 27	March 17 March 17 April 17	139.3 127.9 137.8
1936.....................	March 3 March 4 March 5	March 4	March 4 March 4 March 5 March 19	39.0 116.1 44.4 125.1
1937.....................	March 7 March 17 March 31 April 11 April 12 April 14	April 5	March 9 March 14 March 14 March 20 March 20 March 25 March 28 April 3 April 9	26.8 8.1 82.0 103.3 114.6 119.4 116.3 140.5 152.8

Stage 7: Mature sperms free in the lumen; breeding condition—

Volume range = 82 mm.³–263 mm.³; average volume (22 testes) = 137.92 mm.³; photomicrographs, plates 13 and 14.

The fully metamorphosed sperms are now closely packed in bundles of about seven to ten, which radiate from the lumen, now at its maximum size. The triangles between the tubules contain blood vessels as well as interstitial cells. True connective-tissue cells are present. The tunica albuginea is so thin that its nuclei are almost impossible to see. In six out of seven testes sectioned, even in one with a volume of only 82 mm.³, I saw mature sperms free in the lumen. Whether birds with testes as small as 82 mm.³ are actually capable of copulation is uncertain. The median dates for copulation fall when most of the testes average above 100 mm.³ (table 6), so probably the testes reach a little larger size before mating takes place. Bissonnette and Chapnick (1930) also found mature sperms free in the lumen in starling testes over 2000 mm.³ in volume. Rowan (1929), however, found no free sperms in the testes of a breeding

junco. Although the volume range of breeding testes is wide, the only visible histological difference I could find between the largest and the smallest was that in the smaller the lumen and the spaces between sperm bundles were crowded with cytoplasmic bodies, cast off by the metamorphosing spermatids.

With the exception of the two extremes, with volumes of 82 mm.³ and 263 mm.³, respectively, the volumes of mature testes range from 101.85 mm.³ to 197.30 mm.³ The average, excluding the extremes, is 134.49 mm.³

SUMMARY OF STAGES

By the time the testis reaches about 19 mm.³ in volume, all cell generations from spermatogonia to spermatids are present. From then on, development consists for the most part of metamorphosis of the spermatids, their grouping into bundles, and the accompanying enlargement of the testis.

The stages in the Nuttall sparrow correspond roughly to those in the house sparrow, junco, and starling, as described by the authors just quoted. As might be expected, they do not show such close similarity to those of the starling as to those of the other two species. The main points in which the recrudescence stages in the Nuttall sparrow differ from those of the starling are: (1) absence, in inactive testes, of "interstitial cells with well-stained nuclei and granular cytoplasm"; (2) much less distinct tunicae propriae; and (3) much less dense and smaller amounts of pigment. (Pigment, although present in a few of the gonads I have sectioned, is so small in amount and irregular in distribution that I have not made any special study or record of it.)

REGRESSION TO WINTER CONDITION

Regressive stages are not used in the present study and will not be fully described. One testis of 12 mm.³, collected July 20, 1937, after the last brood had been fledged and close to the beginning of molt, had degenerating sperms in the lumen, but still showed entire primary spermatocytes and spermatogonia (photomicrographs, plate 15). Between the tubules were connective-tissue cells and others resembling interstitial cells, except that the nucleus was not truly spherical but irregular in outline. A still later stage, exemplified in a testis of 4.7 mm.³ volume collected July 20, 1935, showed a great deal of debris in the lumen; all cells, except the single outermost row of spermatogonia, showed degeneration (photomicrographs, plate 16). The intertubular material and the tunica albuginea were thicker even than in winter testes. A few cells resembling interstitial cells were present.

INDIVIDUAL VARIATION

The gonad curve shows that, especially in the period of rapid rise just before breeding, individual birds collected on the same day vary substantially in size of gonads. The greatest variation of which I have record is that for March 4, 1936, when two specimens were collected with testis volumes of 52.3 mm.³ and 122.5 mm.³, respectively. Birds at this period of course also vary in histologic condition. The bird with the smallest gonads on a given day is most often a bird-of-the-year, but not always.

TENDENCIES IN THE TESTIS CYCLE OF THE FIRST-YEAR MALES

The winter condition in "immature" birds (that is, those which have not yet bred) is a little different from that of the adults; the testis is apt to be smaller as a whole, and each tubule within it is smaller, whereas the small spermatogonia are arranged in a more simple and well-defined row. Loisel (1900) found that the testes of immature house sparrows were smaller than those of adults, but Rowan (1929) states that such a difference in juncos, if it exists, is very slight. Also, the immature birds stay in the winter condition longer on the average than do the adults, but this, like breeding behavior, is not a rule which applies to all individuals. As Loisel (1900–1901) says, immature birds may differ greatly in age, and this may explain why some mature earlier than others. Since first-year birds may mate with adults, rigid time barriers between the sexual rhythms cannot exist. For this reason first-year birds are included indiscriminately in the graphs of behavior and development.

RATE OF DEVELOPMENT OF THE TESTES

The rate of testis development, from the first change from inactive condition to breeding, is analyzed for 1936–37 and 1937–38 in table 7. In both years the rate is slow at first, then rapid, then slow again. This tends toward the sigmoid curve characteristic of growth-rate graphs. Although this curve is composite, there are sufficient items to give us a close approximation of the curve of testis enlargement for one individual.

ANNUAL VARIATIONS IN GONAD CYCLE

STAGE 5

Variation in date.—I can establish the fact that identical histologic stages in the testis show year-to-year differences in date. The point where one or more gonads filled with primary spermatocytes in synapsis occur (Stage 5) is the earliest point in the cycle which is represented by sufficient material to be comparable in all four years. A number of gonads have been sectioned and investigated at, and close to, this point, as shown in the graphs (figs. 15–19). It is unfortunate that in 1936 only four gonads were collected at this point, but, as will be shown later, these are consistently related to the rest of the cycle and establish the point with reasonable accuracy. The approximate dates for the appearance of one or more gonads in Stage 5 are as follows: in 1936, January 12; in 1938, January 27; in 1934, January 28; in 1935, February 8; and in 1937, February 15.

In 1935 the first gonad in Stage 5 occurs on February 1; but, since its volume is considerably smaller than the first gonad in Stage 5 collected in other years, I allowed several days for it to reach a comparable volume.

Variation in both rate and starting point.—The fact that Stage 5 comes at different dates each year means one of three things: that there is a variation in the time of earliest change (when interstitial cells appear) only, or in the subsequent rate of development only, or in both. Comparison of the two

years 1936–37 and 1937–38 (figs. 18 and 19) shows conclusively that the interval from first change to Stage 5 must be widely variable in length. In 1937 and 1938, for example, birds with testes of almost identical average volumes (1.44 mm.³ and 1.49 mm.³) were taken on January 6–8 and on January 9, respectively; yet the rates of subsequent development diverged so sharply that Stage 5 was not reached until February 15 in 1937, whereas in 1938 it was

TABLE 7

RATE OF DEVELOPMENT OF TESTES

Period of Fourteen Days	Number of Testes	Volume Range (mm.³)	Volume Average (mm.³)	Percentage of Increase over Previous Two Weeks
		1936–1937		
December 28–January 10.....	7	0.41– 2 36	1.29	....
January 11–24...............	5	0.80– 2.09	1.48	14.7
January 25–February 7	5	1 83– 4.00	3.11	110.0
February 8–21...............	4	2.22– 9.13	6.00	92.9
February 22–March 7.......	5	2 67– 41.10	12 01	100.1
March 8–21.................	5	8.11–114.60	66.99	457.7
March 22–April 4...........	3	116.30–140.49	125.40	87.2
April 5–18.................	1	....	152 75	21.8
		1937–1938		
November 4–17.............	3	0.54– 0.84	0.72	....
November 18–December 1...	1	....	0.17	....
December 2–15.	2	0.59– 1.01	0 80	....
December 16–29...........	5	0.88– 1.27	1.08	....
December 30–January 12....	3	0 95– 2.03	1.19	37.2
January 13–26..............	5	0.88– 3.93	2 32	53.6
January 27–February 9......	3	8.03– 16 08	12.40	434.9
February 10–23............	3	8.03– 42 08	19 93	60.7
February 24–March 9........	2	51.32– 70.71	61.02	206.7
March 10–23................	3	107 00–126 66	117.31	92.2

reached by January 27. The contrast is still more marked if we compare the average volumes for these dates. On February 15, 1937, the average testis volume of four birds was only 6 mm.³; on January 27, 1938, the average testis volume of two birds was 10.21 mm.³ If we interpolate, we find that a testis volume of 6 mm.³ would have been reached in 1938 by January 25, 21 days earlier than in 1937. The rate of testis volume increase averaged only .12 mm.³ per day in 1937; that of an identical segment in 1938 averaged .41 mm.³ per day, a rate over three times as fast as in 1937.

Variation in starting point, on the other hand, is evident as between 1935–36 and three other years, though by less direct and satisfactory evidence. If the time of beginning had been the same in 1935–36 as in 1936–37 (that is, not before January 1), the period from first change to Stage 5 (which we

know took not less than 46 days in 1936–37, not less than 30 days in 1934–35, and not less than 25 days in 1937–38) would have been compressed to 12 days in 1935–36. This is very nearly proof by *reductio ad absurdum* that the time of first change is variable.

Thus the Nuttall sparrow fails to show the "eminent regularity" from year to year in date of incidence and rate of recrudescence of the testes which many authors assume to be generally characteristic of the cycle in wild birds (for example, Rowan, 1929, p. 175) and which appears to be assumed by Bissonnette and Chapnick (1930).

FIRST COPULATIONS

The annual differences in testis development are reflected in behavior. The median dates for first copulations of the banded pairs show annual variations in the same direction and to about the same degree as do the dates of Stage 5,

TABLE 8
FIRST COPULATIONS

Year	Number of Pairs	Median Date	Extremes
1936.....................	3	March 4	March 3–5
1934.....................	1	March 11	......
1935.....................	4	March 27	March 19–April 11
1938.....................	3	April 3	April 2–10
1937.....................	6	April 5	March 7–April 14

except for 1938 when, as explained below (p. 74) extraordinary weather conditions on the verge of nesting time prevented copulation from taking place until long after the testes were fully developed, and threw the year out of sequence.

The difference between 1936 and 1937 is substantiated by differences in dates of first copulation of the same pair (xiii):

YEAR	FIRST COPULATION	DIFFERENCE	MEDIAN DATE FOR POPULATION	DIFFERENCE
1936............	March 4	} 38 days	March 4	} 32 days
1937............	April 11		April 5	

FIRST EGGS

The dates for first eggs have been graphed for all five years (fig. 26). The years are arranged not in chronological sequence but from earliest to latest, according to the dates of the reproductive stages. There are wide annual differences between the median dates of first eggs, always in the same direction and of the same order of magnitude (again with the exception of 1938) as those already described for Stage 5 and first copulation.

These differences are substantiated by the fact that I have first egg dates for a single pair for three years and for two other pairs for two consecutive

years. These show year-to-year variations, always in the same direction as, and usually of a similar order of magnitude with, the population as a whole.

These females were adults except for female I, which was a first-year bird in 1934.

TABLE 9

FIRST EGGS

Year	Number of Females	Median Date	Extremes
1936	7	March 11	March 3–17
1934	6	March 22–23	March 21–26
1935	6	April 4	April 3–18
1938	5	April 7	March 31–April 14
1937	9	April 13	March 25–April 20

TABLE 10

FIRST EGGS: CONSECUTIVE YEARS FOR THE SAME PAIRS

Pair	Year	Date of First Egg	Difference	Median Date for Population	Difference
I	1934	March 21		March 22–23	
	1935	March 31	10 days	April 4	12–13 days
	1936	March 11	20 days	March 11	24 days
II–IV	1935	March 24		April 4	
	1936	March 12	12 days	March 11	24 days
XIII	1936	March 12		March 11	
	1937	April 13	32 days	April 13	31 days

DISCUSSION OF ANNUAL VARIATION

We find that the intervals between the median dates for the attainment of Stage 5 and the median dates for first copulation for 1935, 1936, and 1937 show a maximum variation of only five days, which is very slight, considering that the material is insufficient to give perfect average dates.

YEAR	APPROXIMATE DATE OF STAGE 5	MEDIAN DATE OF COPULATION	INTERVAL
1935	February 8	March 27	47 days
1936	January 12	March 4	52 days
1937	February 15	April 5	49 days

As has been said, the extraordinary late conditions in 1938 upset the behavior phenomena of the latter part of the cycle.

The interval between Stage 5 and the first egg for each year is, again with the exception of 1938, equally consistent, with a maximum variation of only five or six days.

It follows from this that intervals of a similar order of magnitude are to be found from year to year between the time of appearance of the first gonads in Stage 5 and the median dates for first copulations and first eggs.

YEAR	APPROXIMATE DATE OF STAGE 5	MEDIAN DATE OF FIRST EGGS	INTERVAL
1934	January 28	March 22–23	53–54 days
1935	February 8	April 4	55 days
1936	January 12	March 11	59 days
1937	February 15	April 13	57 days

Thus, up to and including 1937, there was every reason to believe that intervals of a similar order of magnitude were to be expected from year to year between the time of appearance of the first gonads in Stage 5 and the median dates for first copulations and first eggs; in other words, that the parts of the reproductive cycle subsequent to Stage 5 were relatively, if not absolutely,

TABLE 11

STAGE 5, FIRST COPULATIONS AND FIRST EGGS

	Pairs of Years		Difference between Pairs of Years	Maximum Variation in Differences
	1934	1935		
Stage 5	Jan. 28	Feb. 8	11 days	
First copulation	....	....	......	2 days
First eggs	Mar. 22–23	Apr. 4	12–13 days	
	1935	1936		
Stage 5	Feb. 8	Jan. 12	27 days	
First copulation	Mar. 27	Mar. 4	24 days	4 days
First eggs	Apr. 4	Mar. 11	23 days	
	1936	1937		
Stage 5	Jan. 12	Feb. 15	34 days	
First copulation	Mar. 4	Apr. 5	33 days	2 days
First eggs	Mar. 11	Apr. 13	32 days	
	1934	1936		
Stage 5	Jan. 28	Jan. 12	16 days	
First copulation	....	....		5 days
First eggs	Mar. 22–23	Mar. 11	11–12 days	
	1934	1937		
Stage 5	Jan. 28	Feb. 15	18 days	
First copulation	....	....		3–4 days
First eggs	Mar. 22–23	Apr. 13	21–22 days	
	1935	1937		
Stage 5	Feb. 8	Feb. 15	7 days	
First copulation	Mar. 27	Apr. 5	9 days	2 days
First eggs	Apr. 4	Apr. 13	9 days	

invariable in duration. Indeed this still appears to be true, in so far as testis development is concerned, for the record-breaking rains and accompanying cold which occurred following January 27 in 1938 had no perceptible effect on the growth curve of the testes, which continued in a manner strictly characteristic of the previous years. When, however, full breeding condition had been attained (March 13), it was accompanied by none of the usual parallel phenomena of behavior, which were delayed about three weeks.

It was interesting to observe that, in spite of the physiological condition which had been reached, the birds were not bound to the wheel of their reproductive cycle to the extent of being forced to breed under conditions impossible for nesting and rearing of young and that, although the hidden physiological development of the male is little, if at all, susceptible, the behavioristic end-results were modifiable by external conditions even at so late a stage. These circumstances will be discussed more fully in connection with the climatic correlates of the cycle.

CONCLUSION

Since, then, the annual differences in time of occurrence are each year alike for these later stages and events in the reproductive cycle, it follows that some common cause must exist, of external origin and annual variation. Since in four out of five years the intervals from Stage 5 to copulation and egg laying have been shown to be of the same length but to fall between different dates each year, it follows that the factors determining the annual variations must complete their operation before the attainment of Stage 5—that is, before the testes reach a volume of 5 mm.[3]

The fact that the time of first change is variable indicates that at least part of the period when the hypothetical external factors are operative must come before the first change. On the other hand, the fact that the length of the interval from first change to Stage 5 is variable indicates that at least part of the period when the external factors are operative must come after first change.

I have to depend upon the meteorological correlations, as treated in the ensuing section, to find out both how long before the time of first change the external factors may begin to influence the time of commencement and the early rate and also how long after first change the influence of such factors may continue to be operative. It cannot apparently continue, in any perceptible degree, after the occurrence of Stage 5 unless, as in 1938, abnormal conditions render the concomitant behavior physically impossible. That is hardly, however, the type of modifying agency of which I am in search.

CLIMATIC CORRELATIONS OF THE GONAD CYCLE IN NUTTALLI

INTRODUCTION

With so much established, it is possible to turn from the history of physiological change to the parallel environmental conditions and the correlations between the two. The first and most important fact is that the period preced-

ing and accompanying early testis development is not one of rapid change and amelioration such as we associate with springtime in north-temperate latitudes. It covers the time of greatest depression when all physical conditions are most inclement and the hours of daylight are at a minimum or increasing at less than a minute a day. A "threshold" for early testis change would have to be a negative threshold, a requisite degree of severity rather than improvement. For this statement, except for its obvious absurdity, a reasonable argument could be prepared. If we could, as actually we cannot, detect the least amelioration of conditions during the weeks following the shortest day, we should be faced with the fact that identical differences prevailed just before. For weeks daylight changes remain so small as to be negligible, considered as dynamic factors. Physiological balance could hardly be adjusted to variations of a minute a day, which may be obliterated or enhanced many times over by weather conditions or the chance of a roosting place.

As is evident in figure 18, in 1937, when the earliest stage is best represented, the starting point of the testis change must have come at least several days before January 6, when one gonad was collected which had reached Stage 4, with a few primary spermatocytes in synapsis. Since in 1937 the whole cycle was very late, it is probable that the start was also late. There is every reason to suppose that in 1936, at least, the start took place much earlier. Therefore the average time of earliest testis change is close to the shortest day of the year. Light, from its minimum up to January 6, is increasing at a far slower rate than either Rowan (1929) or Bissonnette (1930) found to be necessary for artificial stimulation, though it is hardly necessary to seek experimental evidence of the futility of so small an increment over so brief a period. Temperature and total hours of sunshine, as well as percentage of possible sunshine, are varying irregularly about their minima, and precipitation is increasing. It is impossible to suggest reasonable basic external factors as responsible for the threshold changes in the physiology of the bird—changes which must, therefore, be fundamentally dependent upon an inherent annual rhythm.

Since there can be no such fixed threshold in an ascending scale of values, to be reached sooner or later in earlier or later years, and since the fact of variation of the reproductive cycle from year to year is nonetheless unquestionable, the best hope of detecting the controls ultimately responsible, however indirectly, for the variation lies in comparing the environmental conditions during and previous to the cycle in all five years, with the purpose of isolating the variable factors which parallel the variations of the reproductive cycles.

We can eliminate at the start two of the several meteorological factors with available data: first, relative humidity, which shows no suggestion of consistent variation during the periods in question; and second, light, in so far as the theoretical duration of daylight (which has no year-to-year variation) is concerned. It is a cogent possibility, however, that the actual rather than the theoretical amounts of light during the different years might be concerned in the variation in the times of arrival of Stage 5. Yet if this were true, we should

be fairly safe in assuming that the variations would accord with variations in the curves of sunshine and, inversely, with those of precipitation, which they do not. Furthermore, the degrees of cloudiness during the interval from December 21 to date of Stage 5 in all five years do not correlate with the annual variations of the gonad cycle (see table 12).

TABLE 12
PERCENTAGE OF CLOUDY AND PARTLY CLOUDY DAYS,
DECEMBER 21 TO STAGE 5

Year	Cloudy Days	Partly Cloudy Days	Date of Stage 5
1936........................	54 5	31.8	Jan. 12
1938........................	29.7	27.0	Jan. 27
1934........................	28.9	15.8	Jan. 28
1935........................	45.0	22.4	Feb. 8
1937........................	44 6	25.0	Feb. 15

These factors have been dealt with here in order to clear the way for the analysis of the remaining factors which do show both seasonal and annual variations, namely, temperature, precipitation, and sunshine.

METHOD

Almost all daily factors are charted in figures 8 to 12, but it was necessary to reduce this mass of detail to comprehensible units. First, therefore, I calculated for all five years the weekly averages of maximum, minimum, and mean temperature, percentage of possible hours of sunshine, and weekly totals of precipitation. Percentage of possible sunshine was used rather than total hours of sunshine since it was sometimes necessary to compare periods of different day lengths. I then arranged the five years in order, from earliest to latest, according to the dates of the stages of the reproductive cycle (stages of testis development only, in 1938)—that is, (1) 1936, (2) 1934 and 1938, (3) 1935, (4) 1937. This made it evident at a glance whether the meteorological data for individual weeks or groups of weeks of corresponding date for the different years fell into the same order (from hot to cold, sunny to dull, dry to wet) as the years themselves with respect to earliness or lateness of the arrival of Stage 5 and ensuing phenomena. It was then possible to eliminate those periods which did not show perfect "rank-order" correlation and to seek further confirmation of the dynamic importance of those which did.

Because it immediately became evident that, although single weeks would rarely correlate, groups of two, three, and four weeks were going to do so during a certain interval, I decided to use for convenience three periods which left this interval intact and also accorded with the broader natural divisions of the physiological and meteorological cycles. Because the starting point of change in the gonad cycle comes so close to the shortest day in all years, I divided the first two periods at December 21.

Period I.

Prior to December 21. I arbitrarily used November 16 to December 20.

Period II.

From December 21 to the week ending nearest (not necessarily including) the time of appearance of Stage 5; a four- to nine-week period, depending upon the year.

Period III.

From the time of appearance of Stage 5 to the week ending nearest the median date for the first eggs of the year; a seven- to eight-week period for all the years except 1938 when, as has been explained, copulation and egg laying were delayed three weeks after the testes had reached breeding size.

While still engaged in measuring and tabulating the testis development and before turning to the climatic correlates, I predicted that some factor during or just before the period from about December 21 to Stage 5 would yield the closest correlation, since this period includes practically all the annual variation in rate of testis development and hence accounts for the annual differences in date of reproductive readiness in the male. I felt that, if the two methods of approach should confirm one another—that is, if the period containing the segment of testis development most variable in duration should coincide with that during which one or more climatic factors paralleled the order of the years as to dates of Stage 5, first copulations, or first eggs, or if the latter period should just precede the former—the likelihood of having isolated a factor ultimately responsible for the variations in testis development would be very strong.

APPLICATION TO METEOROLOGICAL FACTORS: WEEK-GROUP METHOD

The computations for this analysis are shown in Appendix II, tables 1–7 (pp. 122–128). Four main points should be emphasized.

ABSENCE OF CORRELATION IN PERIOD I

In Period I, mean temperature shows so low a correlation as to be negligible, whereas maximum and minimum temperature, percentage of possible sunshine, and precipitation show no correlation whatever. Variations in these climatic factors during this period are not in the right direction to account for variations in the time of Stage 5 or in the dates for first copulations or first eggs.

HIGH CORRELATION WITH TEMPERATURE IN PERIOD II

In Period II, on the contrary, averages of mean temperature for two-week, or longer, periods show high correlation with the order of years based on the dates of the breeding cycle. If for the moment we disregard 1937–38, the arrangement of all two-, three-, and four-week time units of corresponding date, from warmest to coldest, parallels the order from earliest to latest breeding season in 100 per cent of the cases. This high correlation cannot be accidental, for on the basis of chance alone four units would fall in the 1, 2, 3, 4, order in only 4 per cent of the cases. With the exception of a single two-week period in November-December (Period I), no four-year correlations occur previous to Period II, and no four-year correlation whatever occurs after Period II.

Beyond the simple statement of the probabilities of the four-year rank

order, it is rather difficult to express in mathematical terms the several considerations which lend further support to these correlations. If the correct rank order of each column leaves only some 4-per cent chance of accident, the unbroken sequence of several such columns, their complete absence outside this sequence, the striking contradictions of any such order in Periods I and III, and finally the coincidence of the solid and isolated sequence with the sharply delimited period of variation of testis development, unite to eliminate the possibility of chance or spurious correlation.

The fifth season, that of 1937–38, complicates the problem because during the critical period it lacks variations of sufficient magnitude from two other closely similar years. First, both in temperature and date of Stage 5, it is almost identical with 1933–34, with which I have therefore bracketed it. Second, the temperature of these two years is so close to that of 1934–35 that a single exceptionally cold week in 1937–38 brings the two- and three-week periods which contain it to practical identity with the corresponding periods of 1934–35, though the latter lags somewhat behind with respect to date of Stage 5. Doubtless the deviation from the average temperature level was too brief to be reflected in the physiology of the bird. If, however, we consider the net difference between the daily averages of mean temperatures of 1937–38 and 1934–35, we find that they fall in the correct order by a difference of 0.8° F.

These facts confirm the prediction, based on the variation of testis development during Period II, that some external factor would show the highest correlation during or just before this period.

If we leave out 1937–38, week-group averages of daily minimum temperature will give, with the exception of one two-week period, precisely the same correlation as mean temperature. Maximum temperature gives a lower correlation than minimum, which may indicate a greater sensitivity to night cold than to day heat. Kendeigh (1934), in discussing distribution and other problems, has suggested the importance of night temperature in conjunction with number of hours of darkness.

The year 1937–38 does not correlate for minimum temperature as well as for mean. One four-week period fails to correlate, in addition to the two- and three-week periods already mentioned in connection with mean temperature.

LOW CORRELATION WITH PRECIPITATION AND SUNSHINE IN PERIOD II

Precipitation.—In Period II the only inverse correlation with precipitation is found in the last part of the critical period, where only the two latest years are involved. There is a 50-per cent chance that this is accidental. Furthermore, the earliest of all seasons, 1935–36, is, from December 21 to January 17, also the wettest of all seasons. If dryness were a primary factor in inducing early breeding, we should expect that year, more certainly than any other, to range itself correctly in the series.

Sunshine.—Almost the same thing can be said of correlation with sunshine. There is a slight correlation in the latter part of Period II, between the two latest years only, but in no instance do the time units of corresponding date for all five years, when arranged from sunniest to least sunny, fall in the

order of earliest to latest breeding season. In fact, 1933–34, the second earliest year, is the least sunny of all five.

LOW CORRELATION OF ALL FACTORS IN PERIOD III

In Period III only three out of eleven of the two-, three-, and four-week periods fall in the right order, either for mean temperature or precipitation. Maximum and minimum temperature and percentage of possible sunshine give even lower correlations. The rare correlations which do occur come too late to have any bearing upon the variations in testis development, as indicated by time of attainment of full breeding condition as well as of Stage 5. There arises the possibility, however, that mean temperature and precipitation may exert a secondary effect on the time the first eggs are laid. Nice (1937) worked out a formula showing the relationship between dates when song sparrows laid their first eggs and the level of mean temperature reached about eight days previous to the start of general laying. Less exact correlations of time of nesting and egg laying with temperature and other factors have been found by many workers (Porter, 1908; Burleigh, 1927; Pitt, 1921; Pickwell, 1931; Stevenson, 1932; and others). This evidence is reviewed in detail by Kendeigh (1934) and Nice (1937).

In order to test the effectiveness of the conditions of temperature and precipitation immediately preceding nesting, I arranged Periods III of all five years from earliest to latest according to the median date for first eggs, that is, (1) 1936, (2) 1934, (3) 1935, (4) 1938, and (5) 1937. This differs from the previous arrangement only in one respect: 1938, which was identical with 1934 with respect to testis development and was therefore bracketed with it, now falls between 1935 and 1937, since the median date for first eggs came over two weeks later than in 1934.

This arrangement gives even lower correlations with mean temperature in Period III than did the previous one. None of the two- or three-week periods, and only one of the four-week periods, correlates. Precipitation, however, gives a slightly higher correlation with this arrangement; undoubtedly this was an important, if not the most important, factor in delaying nesting, copulation, and egg laying in 1938. But as far as all five years are concerned, the correlations with both temperature and precipitation are too weak to carry conviction.

Therefore, in spite of the effectiveness, for the culminating activities of the female, of the phenomenally late conditions in 1938, I think the possibility that the mean temperatures and/or precipitation of the period immediately before copulation and egg laying are of basic importance can be ruled out as a general law for the Nuttall sparrow for the following reasons:

a) The percentage of correlation is too low and comes too late to justify our considering either temperature or precipitation of prime importance in modifying the male cycle during this period.

b) Never do all five years fall in the correct order when arranged from warm-to-cold or dry-to-wet, according to mean temperature or rainfall of Period III. The earliest year, 1935–36, never falls in the correct order with

respect to temperature and never, except for one three-week period, with respect to precipitation. In fact, except for a single week, Period III of 1935–36 is consistently colder than Period III of 1933–34 and averages much wetter. Yet the general laying comes approximately eleven days earlier in 1935–36 than in 1933–34.

c) I have already indicated that Period III is of the same length each year with the single exception of the delay of the final phenomena by the impossible conditions of 1938. If temperature or precipitation exerted their effects readily after the beginning of this period (after attainment of Stage 5 of the testes), it would be impossible for this period to be as invariable as it was from 1934 to 1937 inclusive.

This brings out a weakness in my method of defining Period III of the cycle in terms of two separate processes and entities—development of the testis and ripening of the ovary. I can only point to the facts as gathered, which seem to indicate that under any but the most exceptional conditions there was a fixed relation between the time when the male arrived at Stage 5 and the time when the female laid her first egg.

The late, sudden, and rapid development of the ovary and the factors which induce it—whether an inherent rhythm, an external threshold, or stimulation by the male—is a problem of extraordinary difficulty requiring very special study and material over many years. Partly owing to the fact that females are many times more difficult to collect than males, partly to the fact that breeding females are too acutely needed for other purposes to be sacrificed to this special problem, I have not as yet adequate data to attack it. Needless to say, since the female builds the nest and lays the eggs, she controls the final stages, to what degree independently of the male it is impossible to say. It may be said, however, that the spectacular last-minute retardation of nesting in 1938 did not appear, from field observations, to be controlled by the female independently of the male. The characteristic behavior of both sexes was suppressed—song and attempts at copulation no less than trilling and posturing or nest building. Neither bird appeared to be the victim of mechanical compulsion to play its normal part under abnormal conditions, however complete the physiological preparation of the past months.

At any rate, the history of the gonad cycle and its control, analyzed in terms of the stages of the testes, gives us a vastly more detailed picture than we can obtain from the simple changes of the ovary or doubtful suggestions of climatic correlations just before egg laying. We must, for the present at least, be content to understand something of the male and to leave unsolved the problem of the control of the cycle in the female.

Application to Meteorological Factors: Quantitative Method

The purpose of the previous discussion has been, not to compare the meteorological averages of the whole periods, but to analyze them fraction by fraction in such a way as to show the sequence of changes to which the birds were subjected rather than the total quantities of heat, rain, or sunshine to which they were exposed over a long period. The necessity of this is obvious. Two six-week

averages of daily mean temperature, for instance, might be identical whereas the climatic histories of the periods, the conditions the birds were called upon to endure, or the thresholds to which they automatically responded, were profoundly different.

In a more capricious climate than that of California, with greater short-term variability, it would be less likely that the critical periods in question would differ from one another so consistently, with all the week-groups differing as the total quantity of heat differs. In a severe and changeable climate it would doubtless be necessary more often to use broader figures and more average conditions, but in such a climate the interannual differences would usually be far greater and for that reason the rank order even more clear than it is in California. In the present instance, however, it has been shown that temperatures throughout the critical period were relatively uniform. Therefore, we are at liberty to make use of broader figures, expressive of the total amount of heat. These will serve to define the limits of the critical period somewhat more sharply and to express, in broadly quantitative terms, the direct ratio between rate of development and temperature.

I experimented with various delimitations of Period II and found that the most consistent relationship for all pairs of years between magnitude of mean temperature difference between any two years and difference in occurrence of Stage 5 was obtainable if I extended the early limit to December 14, instead of December 21, and set its later limit at the day previous to the date of attainment of Stage 5. I somewhat arbitrarily set the later limit of Period III at the day previous to the median date for first eggs. The three periods thus modified are as follows:

YEAR	PERIOD I	PERIOD II	PERIOD III
1936	Nov. 16–Dec. 13	Dec. 14–Jan. 11	Jan. 12–Mar. 10
1938	Nov. 16–Dec. 13	Dec. 14–Jan. 26	Jan. 27–Apr. 5
1934	Nov. 16–Dec. 13	Dec. 14–Jan. 27	Jan. 28–Mar. 21
1935	Nov. 16–Dec. 13	Dec. 14–Feb. 7	Feb. 8–Apr. 4
1937	Nov. 16–Dec. 13	Dec. 14–Feb. 14	Feb. 15–Apr. 12

This method has one great advantage over the previous one: similar segments of the reproductive cycle in the different years are comparable in their totality whereas in the previous arrangement of the figures only those segments of the periods which chanced to fall between similar dates are directly comparable with respect to rank order.

The daily averages of temperature, precipitation, and sunshine for these three periods are tabulated for all five years (tables 13 and 14). Table 13 demonstrates quantitatively, in a rough way, what was implied in the previous analysis: that in the second period, which must include most of the critical period, the lower the daily average of mean temperature of a given year, the later the date of attainment of Stage 5 in that year. To express it in a different way (table 14), the greater the difference in daily mean temperature between Period II of a given year and that of each of the other four, the greater the difference in dates of attainment of Stage 5 and, with the exception of 1938, the later the median date for first egg. No such constant relationship obtains

TABLE 13

Averages of Temperature, Sunshine, and Precipitation for Periods I, II, and III for the Different Years

*Year	Temperature† (deg. F.)									Percentage of Possible Hours of Sunshine†			Precipitation† (in inches)		
	Mean			Minimum			Maximum								
	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III
1935–1936	54.5	51.4	53.3	48.4	45.7	46.2	60.7	57.1	58.8	56.8	55.8	69.1	0.028	0.199	0.195
1937–1938	56.4	50.8	52.1	50.9	43.9	46.6	61.9	57.5	58.3	47.6	53.8	39.2	.25	.056	.254
1933–1934	55.5	50.7	56.1	47.2	44.3	49.2	63.4	57.1	62.8	18.8	28.3	36.2	.046	.100	.086
1934–1935	54.9	50.0	51.3	48.5	44.1	44.7	61.3	56.0	59.6	47.4	41.6	49.6	.128	.155	.120
1936–1937	54.1	45.0	53.2	46.4	39.7	45.7	61.9	50.3	59.4	65.4	37.8	51.5	0.001	0.214	0.185

* Years arranged according to date of Stage 5.
† Daily average.

for Periods I and III. For example, in Period I, 1937–38, 1933–34, and 1934–35 are all warmer than 1935–36, yet the date of Stage 5 in these three years is from 15 to 27 days later, and the median date of first egg from 11 to 27 days later than in 1935–36. In Period III, 1934 is consistently warmer than 1936, yet the median date for first egg is 11 days later.

TABLE 14

MAGNITUDE OF DIFFERENCES IN MEAN TEMPERATURE AND IN DATE OF STAGE 5

Pairs of Years	Period I Temp. Difference	Period II Temp. Difference	Stage 5 Date Difference	Period III Temp. Difference	First Eggs, Difference in Median Date
1936 and 1938......	+1.9	−0.6	−15 days	−1.2	−27 days
1936 and 1934......	+1.0	−0.7	−16 days	+2.8	−11 days
1936 and 1935......	+0.4	−1.4	−27 days	−2.0	−24 days
1936 and 1937......	−0.4	−6.4	−34 days	−0.1	−33 days
1938 and 1934......	−0 9	−0.1	− 1 day	+4.0	+16 days
1938 and 1935......	−1.5	−0.8	−12 days	−0.8	+ 3 days
1938 and 1937......	−1.4	−5.7	−19 days	+1.1	− 6 days
1934 and 1935......	−0.6	−0.7	−11 days	−4.8	−13 days
1934 and 1937......	−1.4	−5.7	−18 days	−2.9	−22 days
1935 and 1937......	−0.8	−5.0	− 7 days	+1.9	− 9 days

NOTE: The temperature difference of each pair is expressed in terms of the value (+ or −) of the second year (the later year as to date of Stage 5).

Neither maximum nor minimum temperature gives as consistent a correlation as mean temperature in Period II, although minimum temperature approaches it. Neither shows any correlation in Period III. Neither sunshine nor precipitation gives this relationship in any of the periods. The year 1935–1936, the earliest as to date of Stage 5, is second wettest of all years; 1933–1934, ranking third as to Stage 5, is the least sunny.

AN ALTERNATIVE TREATMENT OF TEMPERATURE

If the quantity of data warranted a greater degree of exactitude, it would be possible to analyze temperature in a number of other ways and obtain still more accurate definition of the period when temperature correlates with the reproductive cycle. With the present margin of probable error, however, much further progress is impossible. Nonetheless, I tried a single alternative treatment, depending on the number of days of mean temperature above 50° F. and of maximum temperature above 55° (Appendix II, tables 4 and 5). The number of days with mean temperature above 50° showed a slightly higher correlation with two-, three-, and four-week periods than did weekly mean temperature during Period II, since 1938 always falls in its proper place. On the other hand, the number of days of maximum temperature above 55° gave a lower correlation than did weekly averages of maximum temperature during Period II.

COMBINATION OF TEMPERATURE WITH PRECIPITATION AND SUNSHINE

Although temperature shows by far the highest correlation of all three factors, it is more than likely that a combination of temperature with precipitation or sunshine or both might explain, better than temperature alone, the yearly differences in the time of attainment of Stage 5 and in the dates for first copulations and first eggs.

It must be remembered that, on the average in the climate in question, winter cold is usually accompanied by cloudiness and rain. Therefore it would not be possible, should all three correlate positively with the order of the reproductive periods, to conclude that all three were equally involved. On the other hand, negative correlations become doubly significant. Since, with both sunshine and precipitation records, we have at least one year which is enormously out of order and contradicts by a huge percentage both the order of breeding periods and the order of temperatures, we may reasonably conclude that those climatic factors are by no means the basic determinants of favorable or unfavorable conditions, though, as will be discussed below, they may be of some importance in combination with temperature in controlling the time of breeding.

I have prepared a crude diagram (fig. 30) indicating the relative positions of the whole interval from December 21 to the day before the attainment of Stage 5 for the five years for temperature, precipitation, and sunshine. This shows that the difference in climatic factors between any two years always consists of variation in temperature combined with one or both of the other meteorological factors.

First, Period II of the earliest year, 1935–36, is more favorable than that of the next earliest year, 1933–34, with respect to both temperature and percentage of possible sunshine. The relation between the two years in dryness, however, is reversed, 1933–34 being far drier than 1935–36. Second, Period II of 1933–34 is more favorable than that of either 1934–35 or 1936–37 both in temperature and dryness. Here the relationship with respect to sunniness is reversed, 1933–34 being least sunny of all four years. Third, Period II of 1935–36 is more favorable than that of either 1934–35 or 1936–37 as far as all these factors are concerned. It is not to be understood that such diagrams as figure 30 or table 1 in Appendix II would place every freak year in flawless rank order.

In other words, the whole burden of the evidence which I have been able to accumulate for the factors controlling the annual variation in breeding time under natural conditions points to this fact: that the control is not exercised through any single obscure or elusive factor but rather through a combination of those obvious factors, of which temperature is the most important, which common sense would at once select as making for conditions easy or difficult, favorable or unfavorable, for the life and activities of a warm-blooded animal. The principal object of this part of the present research is to provide scientific evidence of this influence, its potential magnitude, and especially of the time, duration, and degree of susceptibility of the organism.

FURTHER EVIDENCE ON THE LIMITS OF THE PERIOD OF EFFECTIVENESS
OF CLIMATIC FACTORS

It is important to note that temperature does not show any correlation for any combination of two-, three-, or four-week periods prior to December 21, and that the average mean temperature for the whole period does not correlate if the early limit of Period II is extended prior to December 14. Neither precipitation nor sunshine shows any correlation for any part of the period prior to December 21. That is to say, there is no agreement between the order of corresponding time units in Period I when arranged from warm to cold, dry to wet, sunny to dull and the order of the five years when arranged according to the dates of Stage 5. Therefore, the period when temperature combined with sunshine or precipitation or both begins to be effective in modifying testis development does not begin much, if at all, before December 14.

There is no climatic correlation with annual variation in first testis change before December 14. If we allow a few days' lag between cause and effect, the variation could hardly become evident earlier than the last week in December. Now we know that the first testis change in the latest year, 1936–37, occurred about January 1. If the point of beginning was shifted from year to year, it had to occur, then, within this narrow range of ten days or so. The early limit of this range is set by the fact that variations in temperature and other factors do not begin to correlate with time of breeding; the late limit by the fact that in the latest year the first testis change came by January 1. Even if we assume that in 1935–36, the earliest year, variations in temperature shifted the point of beginning of testis development as far forward as December 21, and that in 1936–37 they shifted the point of beginning to January 1, this accounts for only ten of the thirty-four days' difference in the two years between the time of attainment of Stage 5 (January 12 in 1936 and February 15 in 1937). The remaining difference of 24 days must be explained on the basis of modification of rate, rather than beginning, of testis development.

Having roughly established the beginning, it remains, if possible, to establish the end of the period of effectiveness of external factors—to find out when they cease to affect the rate of development. Table 1 in Appendix II shows that in all years the spectacular temperature correlations stop after the week including the attainment of Stage 5, when there follow several weeks which show no correlation. Therefore, in theory at least, temperature should not continue to modify the rate of testis development after about the attainment of Stage 5. Furthermore, my data up to 1937–38 indicated that the period from Stage 5 to copulation and egg laying was substantially invariable. In the latter part of Period III certain minor correlations with temperature occur again but are much lower than in any part of Period II. Their insignificance has already been pointed out.

I was fortunate finally to have at my disposal, in the meteorological data and the breeding cycle for 1938, a natural test of the problem of the susceptibility to modification of the later breeding stages which could hardly have been made more perfect under experimental conditions. This showed that,

although it was practically impossible, as previous years had shown, to modify the rate of the later development of the testis, abnormal conditions, if extreme enough, could inhibit—whether by direct effect on the male or through the suppression of correlative female development or behavior—all courtship, nest building, and copulation, for a period of two to three weeks. Period II ran its course with the usual correlation with the climatic position of the season among the five years. Ensuing conditions of phenomenal severity failed to modify the rate of testis development during Period III.

On January 27 there began the longest period of continuous precipitation ever recorded on San Francisco Bay. The unprecedented rains, with consequent low temperatures, lasted until February 14, and an almost equally heavy downpour continued for a large part of the time until after March 13. By that time the males, whose testis development had been quite unaffected, were ready to breed as far as gonad size was concerned, and copulation and nest building should therefore have been observed. Nonetheless, all breeding behavior was delayed from two to three weeks, until fair weather returned following March 24. First observed copulation occurred on April 2, and the median date for first egg fell on April 7.

Summary and Discussion of the Effects of Climatic Factors

1. None of the external factors so far analyzed can be thought of as initiating the first changes in testis development, because these take place during the most inclement time of the year and, in 1936–37, occurred in the midst of the most severe conditions recorded for fifty years. Therefore we cannot define any set of minimum conditions, even in the critical period of testis development, which are necessary to enable the gonad cycle to initiate and run its early course. Indeed, the circumstances in 1937 suggest that the level of such conditions would lie far below any to which the birds might be subjected in nature.

2. Nonetheless, marked annual variations in certain stages of the gonad cycle do occur. Their degree of correlation with variations in mean temperature justifies the hypothesis that, as far as the Nuttall sparrow is concerned, temperature is the most important single factor lying at the ultimate source of annual variations of the gonad cycle.

I do not intend to say that the variations in testis development are necessarily brought about by a direct physiological effect of temperature. The questions of internal mechanism or of the long series of external factors which may lie between the basic physical conditions of the environment, which we have studied, and the responses which become manifest in the birds' condition or behavior are unlimited in scope and complexity and can hardly form part of a general study of the annual cycle. It is the naturalist's problem to allocate these phenomena in the cycle of nature and to detect the basic, ultimately dynamic, correlatives. Then, and only then, can the more exact sciences be brought intelligently to bear on the problems of wild-animal life, distribution, and evolution.

It may be said in passing, however, that for the variations in these stages of

the gonad cycle no obvious external intervening factors present themselves. Insect diet certainly does not begin until incubation is well advanced. The lawns on the campus and over large areas of the habitat of the local population are kept green and tender the year round, and the shrubbery consists almost entirely of evergreen plants. The birds are largely graminivorous but are also, like all the species of *Zonotrichia*, voracious green-grass eaters. Such food, as well as nesting sites and cover, is maintained in constant and uniform abundance and freshness. There is no reason to expect any important change in the relatively small number of seeds consumed or at least none which coincides with important epochs in the cycle of reproduction. The large number of stomachs in my possession have not yet been analyzed, but years of close-range observation have disclosed no variation in feeding habits other than an emphasis on berries in the fall and the usual swing to insects with incubation or the hatching of the young. These changes are many months removed from the segment of testis development which shows annual variation. The cycle of birds living under the somewhat artificial conditions just mentioned corresponds perfectly with that of the population of the adjacent wild land. Vertebrate animals in nature (whatever physiological upsets may be effected in the laboratories) are obviously controlled by deep-seated rhythms of which the annual variations are broad and common to large groups; they are resistant to the limited or microclimatic conditions to which plants respond so readily.

3. Temperature does not correlate with gonad development during all parts of the reproductive cycle, but only during a particular critical period from about the shortest day in the year to about the attainment of Stage 5, the period of the first rapid and considerable increase in the size of the testis.

4. Analysis of temperature during this period indicates that mean temperature may be more significant than maximum or minimum and that the number of days above 50° for varying periods give slightly higher correlations than do averages of daily mean temperature. The averages for two- to four-week periods correlate best with the annual shifts and modifications of the reproductive cycle.

5. Although variations in precipitation and sunshine do not by themselves give high correlations with annual variations in breeding time, the comparison of all three factors for the five years indicates that a correlation of mean temperature with precipitation or sunshine or both is more significant than temperature alone. General clemency during Period II is what seems to be most important. It seems nearest to the truth, then, to think of the gonad cycle as the expression of an inherent annual rhythm, suggested in general terms by Bissonnette (1937), which may be modified in part by environmental conditions but is by no means entirely dependent upon them for its beginning or its general subsequent course. Exceptionally favorable temperatures, combined with one or more other favorable factors, may allow the cycle to proceed at a rate limited only by the hereditary make-up of the bird; exceptionally unfavorable temperatures can hold back the same hereditary process, the course of which, nonetheless, under any conditions within the scope of the

climate, is inevitable and becomes harder and harder to hold back as the season advances.

A difference of 3.3° F. (perhaps aided by a variation in amount of sunshine) between two-week periods at the beginning of the critical period correlates with the difference (16 days) in time of attainment of Stage 5 between 1935–36 and 1933–34, the sums of the temperatures of the remaining weeks in the critical period being identical. In 1933–34 two consecutive weeks of mean temperature averaging 47.7° F., beginning at December 14, accorded with a shift in the date of appearance of Stage 5 to about two weeks later than in 1935–36. In 1936–37, on the other hand, an almost identical mean temperature of 47° F., coming a month later between February 8 and 14, had little or no retarding effect. The progress of the testis toward Stage 5 had already begun, even when the weekly mean temperature was only 43° F., and it continued. Even during the week of attainment of Stage 5 the mean weekly temperature was only 49.7° F. (fig. 27).

Nice (1937) describes an analogous situation with respect to time of egg laying in the song sparrow and works out a formula showing decreasing temperature threshold with advance of the season.

Of the results of Rowan (1929 *et seq.*) and Bissonnette (1930 *et seq.*) on captive birds I can only say that, whatever effects may be produced by abnormal lighting, the natural cycle under discussion here cannot depend upon increased light for its beginnings and early course. Any regular change, such as the development of the male during Period III, may of course be correlated with any other simple progressive change, such as the daily increase of spring light. In this instance, however, the light change is absent or negligible during the earlier part of the development and cannot serve to initiate it. The fact that so much early growth and change take place without the aid of any considerable increase in light hardly suggests the probability of the importance of light in later stages. In fact it seems to me extremely doubtful whether the abundant means which have been discovered for upsetting the physiological balance of captive birds should be accepted as possessing any bearing whatever on the factors which control the cycle under natural conditions. As Bissonnette (1937, p. 250) himself says: "No mating or egg-laying under these experimental conditions was observed even in starlings brought to complete sexual maturity as judged by histological criteria. Such activities in these wild birds must be controlled by factors not permitted by the crowded conditions in these experiments and not by mere histological fitness for breeding." Even when experimental methods succeed in inducing mating and egg laying, there is little reason to believe that the phenomena reveal the complex organization of the process in nature.

CONCLUSION

We are faced, then, with the fact of a cycle which cannot be initiated by any external factor unless that factor be found at the point of most severe inclemency and the least progressive change—a cycle which furthermore made its beginning in 1937 in the midst of the most severe conditions to which the population had been exposed for at least half a century. The environment may be

thought of as responsible for variations in the rate and duration of early testis development but only within certain limits set by the hereditary clock-work of the population.

Since, as the years covered by these investigations have illustrated, it is by no means possible to predict a favorable or unfavorable nesting period from a favorable or unfavorable midwinter, it is not easy to see adaptive value in the fact that the obscure beginnings of the cycle are more sensitive to modification than the later stages which are to try the energies of the individual to the limit and constitute the vulnerable period for the race as a whole. It is not likely that such minor histological changes could affect the birds' ability to survive midwinter conditions. Yet the fact remains that it is just these remote conditions which ordinarily determine the period of the critical events which follow two or three months later. What makes no sense from an adaptive or evolutionary point of view, however, seems rational and to be expected when viewed as an isolated phenomenon. A cumulative process of increasing scope, complexity, and energy consumption, probably responding to ever stronger and more undeniable endocrine or other physical impulses, may well become increasingly difficult to arrest. As the events of 1938 demonstrate, the organism and the race are, up to a certain point, protected against extraordinary, late conditions by a safety factor of a different type, the suspension of the behavior which ordinarily accompanies arrival at maximum development.

THE GONAD CYCLE OF PUGETENIS IN RELATION TO THAT OF NUTTALLI

INTRODUCTION

The purpose of this section is to discover the precise contrasts offered by the reproductive cycles of these populations, so that the degree and history of their relationship can be more closely estimated, and the presence or absence of apparent adaptation to their respective environments can be determined.

THE HISTOLOGIC STAGES: IDENTITY WITH NUTTALLI

I have already said that the gonad cycle of those northern migratory populations which we include under the name of *pugetensis* is qualitatively similar to that of *nuttalli* but differs in time of attainment of the successive stages and in rate of development. I have sectioned 73 testes of *pugetensis* with volumes ranging from .23 mm.³ to 162 mm.³ and subjected them to the same treatment and examination as those of the Nuttall sparrow. In so far as I am able to discover, the histologic stages are identical, and the average volumes of testes in each stage are approximately the same. The testes have been graphed in the same way as that described for the Nuttalls (figs. 13, 14, and 20–25).

It is especially significant that in Stages 4 and 5 the functional interstitial cells, which Rowan (1929) suggested might be intimately connected with migration, are, in so far as I can estimate, just as numerous in the testes of the strictly resident *nuttalli* as in the *pugetensis* which are about to migrate (see

photomicrographs, plates 8, 9, and 17). This histological identity is marked by the sharpest contrast in behavior. Attainment of Stage 4 in *nuttalli* coincides with the restriction of each pair to a portion of its wintering ground, the segregation into pairs of previously unmated birds, and the beginning of territorial jealousy. In *pugetensis,* on the other hand, the attainment of Stages 4 and 5 is accompanied by none of these phenomena but by the departure and flight of perhaps a thousand miles to the breeding grounds. By the time of final settlement on breeding territory the testes of *pugetensis* are eight times the size of those of *nuttalli.* Such a contrast does not, of course, prove that interstitial cells are not involved in, or contributory to, the impulse to migrate but certainly shows that interstitial cells may be not less abundant and active in a resident than in a migratory race and may appear at a similar point in the cyclic history. In both populations radical changes in behavior take place at the time when actively secreting interstitial cells are reaching their maximum number. It seems likely enough that this condition should play some dynamic part in subsequent development. If so, we can only say that, though the end-results are the same, the intervening phenomena are very different. Such histologic changes are deep-seated and probably relatively uniform throughout a large part of the avian world. Subsequent behavior is exceedingly diverse and probably represents the most refined manifestation of incipient variation we shall ever be able to detect. Rowan (1932), in this connection, has come to the conclusion, on the basis of experiments with castrated crows, that gonads are not essential at least to the southward or fall migration.

THE HISTOLOGIC STAGES: VARIATIONS IN DATE AND RATE
BETWEEN PUGETENSIS AND NUTTALLI

RECRUDESCENCE

I can date the time of the beginning of recrudescence in *pugetensis* most accurately in 1934. On January 10 one adult was taken which had reached Stage 2. Out of six adult males collected from January 21 to 25, one was still in inactive condition, four were in Stage 2, and one had achieved Stage 3. On January 31 two more were collected with testis volumes so small (.28 mm.³) as to make it highly probable that they were still in inactive condition. Therefore the average time in that year for the beginning of recrudescence in *pugetensis* is definitely later than in *nuttalli,* since by January 28 all Nuttalls had reached Stage 4 and two had reached Stage 5.

In 1935 an adult *pugetensis* collected January 15 had already reached Stage 3, but two others collected January 30 and 31 were only in Stage 2. In 1936 two adults taken January 12 and 13 and two immatures taken February 19 were still in Stage 2. In 1937 five adults, all in Stage 2, were taken on the following dates: one January 20, one February 8, one February 15, and two February 23. In all four years, then, the *pugetensis* population remained in Stage 2 much later than did the Nuttall sparrows.

The first increase in testis volume came considerably later in *pugetensis*

than in *nuttalli*. In 1935 two Puget Sound sparrows with testes in Stage 2 but near the minimum in volume (.71 mm.³) were collected January 31 and February 1. The last Nuttall sparrow with testes of about the same volume (.65 mm.³) was taken January 20. In 1936 three Puget Sound sparrows taken as late as February 19 had testes still of practically minimum volume (average .51 mm.³). One Nuttall with testes still in Stage 2 (volume 1.00 mm.³), was taken January 12 in this year, but all others, even on the same day, were con-

TABLE 15

VOLUMES OF TESTES IN STAGE 2

(Graphed in figs. 20–23)

Year	PUGETENSIS			NUTTALLI		
	Date	Volume (mm.³)	Last Day Testes in Stage 2 Were Collected	Date	Volume (mm.³)	Last Day Testes in Stage 2 Were Collected
1934................	Jan. 10 Jan. 25 Feb. 13	0.98 0.88 0.52 0.52 1.83	Feb. 13	....	....	(Stage 4 by Jan. 28)
1935................	Jan. 31 Feb. 1	0.70 0.72	Feb. 1	Jan. 12 Jan. 13 Jan. 20	0.85 0.53 0.65	Jan. 20
1936................	Jan. 12 Jan. 13 Feb. 19	0.37 0.49 0.47 0.34	Feb. 19	Jan. 12	1.00	Jan. 12
1937................	Jan. 19 Feb. 7 Feb. 15 Feb. 23	0.47 0.62 0.80 0.95 0.80	Feb. 23	Dec. 28 Jan. 6 Jan. 19	1.09 0.75 0.50 0.80	Jan. 19

siderably larger and further advanced. In 1937 two Puget Sound sparrows were taken February 23 with testes still in Stage 2 averaging only .88 mm.³ in volume. The last Nuttall with testes of comparable volume (.80 mm.³) was taken on January 19 of that year. In 1938 five Puget Sound sparrows with testes averaging .57 mm.³ were collected January 30. This is so close to the minimum volume that we are safe in assuming that little or no increase had taken place. On February 11, seven more were taken with testes averaging 1.05 mm.³ In this year, then, the initial increase came between January 30 and February 11. In the Nuttall, on the other hand, initial increase took place at least before December 25, when the average volume of three birds was 1.09 mm.³ These data are summarized in table 15, which shows the volumes of all testes of both races which were sectioned and found to be still in Stage 2. It is not possible to include 1938 since none of the testes has as yet been sectioned.

ATTAINMENT OF STAGES 4 AND 5

There are even wider differences between *pugetensis* and *nuttalli* with respect to the time of attainment of Stages 4 and 5. The approximate dates for the first gonads in these stages for each year are given in table 16.

TABLE 16

STAGES 4 AND 5 IN PUGETENSIS AND NUTTALLI
(Graphed in figs. 21–24)

Year	Race	Stage 4	Difference in Days	Stage 5	Difference in Days
1935.	*pugetensis*	Mar. 15–20		Not before Apr. 3	
			At least 45 days		At least 54 days
	nuttalli	Before Jan. 29		Feb. 8	
1936.	*pugetensis*	Mar. 5 or before		Not before Mar. 19	
			At least 57 days		At least 67 days
	nuttalli	Before Jan. 12		Jan 12	
1937.	*pugetensis*	Mar. 15		Apr. 3	
			68 days or slightly less		47 days
	nuttalli	Jan. 6		Feb. 15	
1938.	*pugetensis*	Mar. 8		Mar. 27	
			48 days		59 days
	nuttalli	Jan. 9		Jan. 27	

FIRST CHANGE TO STAGE 5 OR MIGRATION

The fact that the first histologic change takes place later in *pugetensis* than in *nuttalli* accounts in large part for the difference in time of attainment of Stages 4 and 5 (a 47- to 68-day difference). The remainder can be accounted for by a demonstrable difference in rate. The smallest average testis volume of Nuttalls collected in 1936–37 is .92 mm.^{3} on December 28. An average volume of .88 mm.^{3} had been attained by the Puget Sound sparrows on February 23. This 57-day difference is undoubtedly due to differences both in time of initial volume increase and in rate but cannot be analyzed because earlier material is not available. If we start with these roughly comparable volumes, we find that the ensuing rates are different. In 1937 the average testis volume of *pugetensis* increased from .88 mm.^{3} to 4.29 mm.^{3} in 39 days. This represents an average rate of 9.9 per cent per day. The rate for a roughly comparable segment of testis development in *nuttalli* was 11.16 per cent per day, repre-

senting an actual change from .92 mm.[3] on December 28 to 5.55 mm.[3] between February 7 and 15. It is quite possible that, owing to limited quantities of material, this record of average testis volume of *pugetensis*, still so close to the winter level on February 23, is too small and that further collecting might have produced one or two "early" individuals which would have raised the average. If so, the rate would be even slower, and the difference between the two races enhanced.

The same procedure for 1937–38 does, in fact, give us a greater difference in rates. An average volume of 1.09 mm.[3] was reached by the Nuttalls on December 25, and an almost identical volume (1.05 mm.[3]) by the Puget Sound sparrows on February 11. It required 44 days for the testes of Puget Sound sparrows to increase from an average volume of 1.05 mm.[3] (February 11) to an average volume of 4.04 mm.[3] (March 27). This is an average daily increase of 6.5 per cent of the initial volume. If we interpolate for *nuttalli* between January 23 and 27, we find that a roughly comparable volume of 4.34 mm.[3] would have been reached by January 24. Since it required 30 days for the Nuttalls, starting at 1.09 mm.[3] on December 25, to reach this volume, the daily rate is 9.9 per cent of the initial volume.

It is impossible to compute parallel figures for 1936 because the average testis volume of the first Nuttalls collected had reached 5.08 mm.[3], but there is every reason to believe that the rate would have diverged much more sharply than in either 1937 or 1938 since the difference as to time of occurrence of Stage 5 was at least 67 days, far more than in either of the later years.

LATER DEVELOPMENT IN PUGETENSIS: STAGE 5 TO BREEDING

Calculation of the rate of later development in *pugetensis* is of course complicated by the fact that, at least among the northernmost breeders, the greater part of it takes place during migration and the first days on the breeding grounds. It is obviously impossible to follow and study any one group, and we have little direct knowledge—though much may be surmised—of the relative positions of breeding and wintering grounds of the different populations. I have data on behavior and gonad condition for birds collected at Berkeley up to the point of departure for several years. I have a number of preserved specimens and skins from Tillamook, Oregon, while migration was in progress in the springs of 1935 and 1936. Finally, I have abundant material and my own observations from Friday Harbor, Washington, covering time of arrival and the subsequent breeding season of 1936; also a considerable amount of material collected at time of arrival from Comox and other points in British Columbia for several years. Through the kindness of Mrs. Forrest Fuller I have also valuable items of information for Friday Harbor for certain other years.

Condition previous to migration.—In 1935, 1937, and 1938, Puget Sound sparrows were collected at Berkeley up to the time of their disappearance. In 1935 only one, among the last collected, had testes as large as 5.26 mm.[3], and most had testes of only 4 mm.[3] or less in volume. In 1937 and 1938 the development before departure was the same, with a single exception each year,

of a bird with testes of 12 mm.^{3} and 9 mm.^{3} volume, respectively. In 1936, owing to my own departure to await the migration in the north, the actual disappearance was not observed, but a similar development was watched until near the time of departure. The most advanced birds had passed 4 mm.^{3} before I left, barely in time to anticipate the arrivals at Friday Harbor. I conclude, therefore, that birds with testes of 4 mm.^{3} to 5 mm.^{3} are on the verge of departure. Except for the two birds just mentioned and one other already discussed, which, presumably on account of an injury, was unable to migrate, none has ever been collected in Berkeley with larger testes, and the development certainly never stands still. The completion of the prenuptial molt and the laying on of the maximum amount of fat may already have taken place in individuals with testes as small as 3 mm.^{3}; thus these developments, although good indicators of imminent departure, are not as reliable as testes above 4 mm.^{3} volume. Average testis volume, for birds which had completed the molt and were at least moderately fat, was 3.66 mm.^{3} in 1935, 3.51 mm.^{3} in 1936, 5.86 mm.^{3} in 1937, and 4.05 mm.^{3} in 1938.

Appendix III shows testis volume for Berkeley birds, beginning from about a month previous to the date of disappearance. Specimens marked with an asterisk are those judged physiologically ready to migrate since they have finished molting, laid on fat, and attained histological Stage 4 or 5.

Material from northern stations.—Tillamook, Oregon: The birds collected at Tillamook unquestionably spent the winter farther south. The observations of Mr. Alex. Walker and Mr. Reed Ferris over many years indicate that, as at Friday Harbor and Comox, a wintering bird is an extreme rarity. In the winter of 1936–37 none was seen at Beaver or Tillamook. In the winter of 1934–35 one immature was collected at Beaver on January 26. In December, 1937, during a week's search by automobile through the coastal regions of Oregon, assisted by Dr. Mary Erickson, I found no white-crowns north of the town of Umpqua, near Roseburg, in the interior, or north of Coquille on the coast. The number, date, and condition of the Tillamook birds is shown in Appendix IV. A discussion of their status will follow in a later section.

Friday Harbor, Washington: I reached Friday Harbor in 1936 ahead of the great influx which occurred on April 10 and found only rare individuals already present. The males collected on, or shortly after, the April 10 invasion were unquestionably destined to breed on the spot. All were singing loudly from conspicuous posts, were restricting themselves territorially, and several such pairs, color-banded within two days after arrival, remained through the breeding season. (Appendix IV.)

Comox, B. C.: The birds collected here on, or shortly after, arrival must also have been part of the breeding population, since this point represents the approximate northern limit of the breeding range. (Appendix IV.)

Condition on arrival at northern stations and the variation of migratory behavior with latitude.—The most significant facts to be deduced from this material are the following: Although times of arrival at northern stations differ but slightly, the more northern the breeding populations, the more advanced the physiological condition of their members on arrival.

This is, of course, what might theoretically be expected if the northernmost populations were likewise the most distant migrants and if all the migratory populations were moved to start north in the spring at the same physiological threshold, correlated with similar environmental sequences. Actually, such a hypothesis, in its broad outlines, is supported by many considerations and by a few facts.

First, there is a single item of concrete proof, if not of the maximum possible migration of the northernmost breeding populations, at least of their very distant migration, namely, the record of a summer recovery near Victoria, B. C., of a Puget Sound sparrow banded in Berkeley, California, during the previous winter (Clabaugh, 1929).

Second, we know that the populations which winter or summer at the extremities of the range make long, if not necessarily the longest possible, migrations. The summer population of the northern extremity must migrate not less than 500 miles (Comox to Coquille or southward), and the winter population of the southern extremity must migrate not less than 750 miles (San Diego to the Oregon line or northward). For these populations a strong migratory instinct is a fact.

Third, we have spring birds arriving at Tillamook, which is only some 150 miles north of the northernmost wintering population, with testes quite regularly as small as, or very little larger than, the "threshold size" at which the migrants leave Berkeley. Now since arriving spring migrants at more northern points prove that enlargement (even up to 78 mm.^{3} in one example and 158 mm.^{3} in another) may take place presumably during migratory flight or at any rate before arrival on the breeding grounds, the obvious conclusion is that the undeveloped Tillamook birds have made a very short flight; that is, that they have hardly left their wintering grounds. My experience at Friday Harbor convinces me that these easily collected singing birds are prospective breeders and that, with this race in these surroundings, one is largely unconscious of the birds of passage. During the ensuing days the testes of the birds successively collected at Tillamook showed a slow normal change in condition and increase in size, with no suggestion of a break or change of population.

Fourth, dates of spring arrival at Tillamook, Friday Harbor, and Comox, though these points cover a latitudinal distance of some four hundred miles, are so close as to make me suspect that more abundant material might show identity. For this there are two possible explanations. It might mean that, of two groups starting from a distant southern point, one had flown faster than the other; such a supposition, however, is pointless and unlikely in the extreme. A far more probable explanation is that there is a fair compensation between distance traveled and those latitudinal and climatic successions which determine time of departure, so that a bird which has flown a thousand miles to Vancouver Island, starting on occurrence of threshold conditions in south-central California, reaches its goal roughly at the same time as, but in a far more advanced physiological condition than, a bird which has flown one hundred and fifty miles to Tillamook, starting with the occurrence of threshold conditions in southern Oregon.

Fifth, even without these more or less concrete indications, we might have surmised as much from the nature of the duality of race. Remembering that the forms in question are morphologically as close as two partially distinguishable groups can be, that they are geographically continuous and show the most complete intergradation, we are forced to think of them not as sharply sundered and differentiated entities, such as might have been separated, differentiated, and recombined in the past, but rather as representing an incipient, by no means finite, degree of probably active divergence. As far as the migratory habit goes, we know that it is never complete, even in the most extreme northern breeding populations; records of odd wintering birds from Vancouver Island, Portland, and Tillamook are unquestionable. It is unthinkable that at the northern part of the residential or mainly residential area or at the southern limit of the mainly migratory area, we suddenly, between one pair and the next, pass from residence to fully developed migration or vice versa. The conclusion that the transition is intergradational rather than abrupt in character is inherent in almost any theory we may conceive to explain the gradual development, or gradual loss, of the migratory habit by the different fractions of the population. Whatever is advantageous in the migratory habit or whatever mechanism is serving to produce or to suppress it probably applies most strongly to the extreme northern or southern breeding populations.

Thus, without relying wholly upon the fact that a single bird flew in the spring from Berkeley to Vancouver Island, there are many considerations which lead us to believe that in general the more northern breeders represent southern winter visitors, say from southern to central California. This latter is a large territorial unit but does not, to judge from data from the northern stations, represent a great difference in time of arrival or in condition on arrival at any single station. Had the banded Berkeley bird been a male and had it left Berkeley at the average testis size of about 4 mm.^{3} (and the range of size at departure is very narrow) and arrived on Vancouver Island likewise at the average size, about 55 mm.^{3}, its gonads would have increased 51 mm.^{3} in about 1000 miles of flight. If it had left Berkeley among the earliest in 1936 and arrived, en route, among the first at Friday Harbor, its flight and the accompanying development would have taken about 15 days. Had it come from Los Angeles it would have been, physiologically, among the upper extremes on arrival; had it come from northern Mendocino County, California, it would then have been among the lower extremes, with corresponding shading of the time consumed. If it had belonged to some more northern wintering population, its migratory instinct would have been weaker or less decisive, and it would never have reached Vancouver Island but might have bred at Tillamook.

I do not mean to say that with mathematical precision the northernmost breeding-population unit must be the southernmost wintering one. It is probable that, in the history of the development of the differentiation within the *nuttalli-pugetensis* aggregate, many accidental circumstances determined the allocation of groups to their exact breeding and wintering grounds. The

banding records in this country and in Europe do not always indicate complete coherence of breeding or wintering groups or a perfect degree of latitudinal arrangement of such populations at both ends of the routes. The most that can be said in regard to *pugetensis* is that, in general, the northernmost-breeding and southernmost-wintering populations are those of longest migratory flight, whereas there is every reason to believe that the habit of residence passes gradually into that of migration in the region of the California-Oregon line.

Breeding: the relative dates.—The differences between the times of attainment of breeding condition in the Berkeley *nuttalli* and the *pugetensis* of various points in the northern part of the range are of smaller magnitude than differences between times of attainment of Stages 4 and 5.

Breeding: 1934.—The Berkeley Nuttall sparrows reached breeding condition in mid-March. One bird with testes of 263 mm.^{3}, far above average breeding size, was taken March 21. One of the pairs on the campus was seen copulating on March 11. Three newly arrived Puget Sound sparrows were collected by Mr. Thomas T. McCabe at Sea Island, near Vancouver, B. C., on April 16, with testes averaging 53.13 mm.^{3} From my experience of the rate of development of the near-by Friday Harbor birds immediately after arrival on their breeding grounds, I should judge that at least ten days more were needed to bring the Vancouver birds to breeding on or about April 26. This means that in the course of the differentiation of the races, a 42-day difference has come into being, with respect to attainment of breeding condition by the males, between populations which breed exactly 1000 miles apart.

Breeding: 1936.—The median date for first copulations for the banded Nuttall sparrows was March 4. On March 5 one adult was collected with testes averaging 116.1 mm.^{3} in volume. At Friday Harbor breeding condition (average testis volume over 100 mm.^{3}) was not reached until April 19–20, when the average of eight birds was 111.67 mm.^{3} This 46-day difference is substantiated by the 49.5-day difference in median dates for first eggs for the same populations (March 11 for the Berkeley Nuttalls and April 29–30 for the Friday Harbor Puget Sound sparrows).

Breeding: 1937.—The median date for the Berkeley Nuttall sparrows was April 13. Through the kindness of Mrs. Fuller I have the record of the first egg of a Friday Harbor Puget Sound sparrow which was banded and watched in 1936. In 1937 this female laid her first egg on May 7. In 1936 she laid her first egg on May 1, within two days of the median date for the 22 pairs observed. If she came as close to the median date in 1937, there was about a 24-day difference in breeding time between the Berkeley Nuttalls and the Friday Harbor *pugetensis*. Even when the Nuttalls were retarded to an extraordinary degree by the severest winter of half a century, a substantial interval elapsed between their breeding time and that of the *pugetensis* of the northern stations.

Rate of development of pugetensis on the breeding grounds.—For the Friday Harbor breeding population at least, the rate of testis development on the breeding grounds, as expressed by actual amount of material produced, was

more rapid than that of the period of migration. In 1936 it required only 9.5 days for the average testis volume of the Friday Harbor breeders to increase from 55.26 mm.^{3}, the average size on arrival, to 121.60 mm.^{3}, the average breeding size. This represents an average daily increment of 6.98 mm.^{3} as opposed to an increase of 3.40 mm.^{3} per day for the testes of the hypothetical bird during its flight from Berkeley to Friday Harbor. This is apt to be deceptive, however, in that it by no means represents an increased rate of cell division. Such comparisons of rates of different segments of development are complicated by the fact that not all the increase in volume is the result of the production of solid matter, for during the metamorphosis of the sperms the relative amount of intercellular space is greatly increased.

It is hardly possible to continue this comparison of rates during and after migration for points farther north because in such instances too much of the growth takes place during migration, too little after arrival on the breeding grounds. Extreme birds arrive almost in breeding condition. The average testis volume of ten birds collected at Comox on April 15 of the same year was 87.47 mm.^{3} The average of six birds twelve days later, on April 27, was 116.2 mm.^{3} This represents an average daily increment of 2.56 mm.^{3} It is possible that breeding size had been reached before April 27; if this is so, the rate would be a little faster.

Relative rates: Stage 5 to breeding.—This period has already been treated in segments for *pugetensis,* but, since there is no natural unit in the life of *nuttalli* which lends itself to comparison with the migratory flight of *pugetensis,* the material will be reviewed here as a unit for purposes of comparison. If we take the hypothetical case of a bird wintering at Berkeley and breeding at Friday Harbor, we find, as has just been said, that the increase in testis size in 1936 would have been from an average volume of 3.16 mm.^{3} on March 15–19 in Berkeley to an average volume of 111.67 mm.^{3} on April 19–20 at Friday Harbor. This represents an average increment of 4.59 mm.^{3} per day. The average daily increase of a roughly comparable segment of development for *nuttalli* is less than half as much—only about 2.11 mm.^{3} per day, that is, from 5.08 mm.^{3} on January 12–13 to 116.1 mm.^{3} on March 5. The average testis volume for March 5 would be less if one immature collected that day were included, but, since copulation was taking place among the banded pairs, I think it is closer to the truth to consider the average volume as 116.1 mm.^{3}

This difference between the later rates explains the fact that in 1936, although the difference between median dates for first eggs was only 49.5 days, the difference of time of attainment of Stages 4–5 was 67 days. If we assumed that the Friday Harbor birds wintered in Berkeley, we could say that they made up part of the time lost in slow development on the wintering grounds by a much more rapid rate of development during migration and the first days on the breeding grounds. This undoubtedly approximates the truth.

Regression in pugetensis and nuttalli.—In spite of the fact that the Puget Sound sparrows reach breeding condition later than do the Nuttalls, their reproductive season is so compressed that regression of the testes begins in late July and early August, roughly at the same time as in *nuttalli.* Table 17

shows testis volumes of adult Puget Sound and Nuttall sparrows collected at roughly comparable dates in the fall of 1936.

Four of the five testes collected at Victoria were sectioned. The largest, collected August 4, was in an advanced stage of regression. All but the outermost row of spermatogonia were degenerating, and the lumen was filled with degenerating cells. The intertubular material consisted of cells with nuclei of various shapes, a few large-spherical, more large-oval, and some small and irregularly shaped. These may represent stages in the transformation of the interstitial cells from the functional to the nonfunctional condition. The other three testes had regressed even further. (See photomicrographs, plates 19 and

TABLE 17

VOLUMES OF TESTES IN NUTTALLI AND PUGETENSIS, FALL OF 1936

Date	NUTTALLI		PUGETENSIS		
	Number Collected	Average Volume (mm.³)	Number Collected	Average Volume (mm.³)	Place Collected
July 12.............	..	....	2	258.37	Friday Harbor,
July 20.............	1	5.74	..	....	Washington
July 23.............	1	0.43	..	....	
July 24.............	1	143.90	..	....	
Aug. 4.............	..	....	1	4.97	Victoria, B. C.
Aug. 5.............	..	....	1	1.51	
Aug. 14.............	2	1.09	..	....	
Sept. 1.............	..	....	2	.97	
Sept. 14.............	..	....	1	.70	
Sept. 27.............	1	0.50	..	....	

20.) The one collected on September 14, the day Puget Sound sparrows were last seen at Victoria, had smaller tubules than the one of August 4, fewer degenerating cells still present in the lumen, and the intertubular material consisted almost entirely of small compact nuclei of irregular shapes, resembling the condition of inactive testes.

By the time, then, that the Puget Sound sparrows are ready to leave their breeding grounds, regression of the testes is almost complete. By the time they arrive on their wintering grounds their testes, if we may judge from volume alone, have already reached the inactive condition. Of the five adults collected in early October of 1934 and 1935, soon after the Puget Sound sparrows had arrived at Berkeley, one had testes 2.05 mm.³ in volume, but the four others had reached an average volume of .52 mm.³, which approximates the inactive condition.

ANNUAL VARIATIONS IN THE CYCLE OF PUGETENSIS

The gonad cycle of *pugetensis* contrasts strongly with that of *nuttalli* in the order of magnitude of the annual variations. In this race—developing, migrating, and breeding as it does at a much later date, after the vagaries of the winter season and during the extraordinarily equable California spring— the annual variations, although in the same direction as those of the Nuttall

sparrow, are much less marked; consequently chances of establishing correlative factors of possible importance are much reduced.

<div align="center">STAGE 4</div>

The three years for which we have material for Stage 4 in *pugetensis* range themselves in the same order as for the dates of Stage 5 in *nuttalli,* with 1936 earliest, 1938 next, and 1937 latest. By March 5 to 7, 1936, six out of seven birds collected had reached Stage 4. Three were sectioned, the others estimated from volume. In 1938 two out of four birds collected March 8 had reached volumes of 2.71 and 3.47 mm.^{3}, respectively, and therefore must have reached Stage 4. In 1937 only two out of five birds collected March 14 had reached Stage 4. This material can be made more closely comparable by interpolation. The birds on the average enter Stage 4 with a testis volume of 2 mm.^{3} In 1936 the average volume of five birds collected February 19 was .85 mm.^{3} By March 5–7 average testis volume of seven birds had reached 2.66 mm.^{3} A simple interpolation between these dates and volumes gives March 1 as the date on which the average volume would have reached 2 mm.^{3} If we treat the figures for 1938 the same way, interpolating between February 22 and March 8, we find that an average volume of 2 mm.^{3} would have been reached March 4, only three days later than in 1936. In 1937, on the other hand, by interpolating between March 14 and 25 we find that an average volume of 2 mm.^{3} would not have been reached until March 17, sixteen days later than in 1936. There is no such contrast between 1936 and 1937 for *nuttalli* at this stage since in 1937 the birds had reached Stage 4 before the severe weather set in.

<div align="center">FAT, MOLT, TESTIS SIZE, AND DEPARTURE</div>

In *pugetensis* the prenuptial molt and the recrudescence of the gonads are accompanied by the assumption of large amounts of fat. This increase is so great that the body weight of adults increases from an average of 26.8 gm. for adult males with no fat to an average of 32.6 gm. for those with the maximum amount, a 21.6-per cent increase. In 1938 the increase took place within six weeks at most, between February 11, when the average weight of six adult males was 26.7 gm., and March 27, when the average weight of six adults was 30.7 gm. But in point of fact a very large part, and the most rapid part, of this increase occurred in the last nineteen days, when the weight increased from an average of 28.5 gm. to 30.7 gm.

I have adopted the five categories for amount of fat used for field work by T. T. McCabe (MS) : "no fat" when the feather tracts and furcula are clean or practically so; "little fat," with small amounts on these parts; "moderately fat" when a substantial amount lies on the tracts and fills the crotch of the furcula; "fat" when the abdomen, as well as the furcula and the tracts, contain quantities of fat; and "very fat" when the abdomen bulges with fat, which also lies on the sides of the neck and body. His final category, "excessively fat," these birds never reach. That my segregation of birds into these categories has been consistent is borne out by the steady increase in body wight as we pass from one group to the next. Adult males with no fat average 26.8 gm. in

weight; those with little fat, 28 gm.; those with moderate fat, 29.1 gm.; fat birds, 29.3 gm.; and very fat birds, 32.6 gm.

The laying on of fat may begin previous to or during the prenuptial molt. Of 22 males collected in January and February which had not begun to molt, 17 had no fat and 5 had little fat. Of 24 molting birds collected from mid-February to April, 12 had no fat, 11 had little fat, and 1 was fat. The most rapid increase comes just at the completion of the molt. Of 27 birds just finishing the molt—that is, birds which had all the new feathers fully grown out except a few on the crown—1 had little fat, 8 were moderately fat, 11 were fat, and 7 were very fat. Of 21 birds which had completed the molt, 6 were moderately fat, 9 were fat, and 6 were very fat.

TABLE 18

ANNUAL VARIATIONS: MOLT AND ASSUMPTION OF FAT

Year	Molt		Assumption of Fat		
	First Sign	First Bird Finished	First Moderately Fat Bird	First Fat Bird	First Very Fat Bird
1936........	Feb. 19	March 5	March 5	March 7	March 7
1938......... ..	Feb. 22	March 20	March 13	March 20	March 27
1937........	Feb. 28	March 25	March 14	April 3	April 3

There is also a fairly consistent relationship between average gonad size and amount of fat. The average testis volume of the no-fat group of adults is 1.54 mm.^{3}; of the little-fat group, 2.28 mm.^{3}; of the moderately fat group, 3.68 mm.^{3}; of the fat group, 4.02 mm.^{3}; and of the very fat group, 5.18 mm.^{3} There is, however, a wide individual variation as to this relationship since a bird with no or little fat may have testes ranging from the inactive level to Stage 4; a bird with moderate fat, testes from Stage 3 to 5; and a fat or very fat bird, testes from Stage 4 to 5.

The annual variations in time of assumption of fat and in beginning and completion of molt for the three years with adequate material are summarized in table 18. Both adults and immatures are included.

The date when the fat and very fat condition is reached coincides with the time of maximum gonad size attained on the wintering grounds and therefore with the time of departure. To judge from the condition of arrivals on the breeding grounds at Friday Harbor in 1936 and at Vancouver in 1934, these great amounts of fat are completely used up during migration. None of the five males collected on the day of the main influx into Friday Harbor had any fat, and they averaged only 27.1 gm. in weight. Of three males collected at Vancouver in 1934, two had little fat and one was moderately fat, but their weights averaged only 26.6 gm.

The Nuttall sparrows may during midwinter lay on a little fat, but no such phenomenon as that described for *pugetensis* accompanies the recrudescence of the gonads. Of 60 males with testis volumes comparable to the Berkeley

pugetensis collected from January to March in all years, 44 had no fat, 13 had little fat, and only 3 had moderate fat. The cycle of the Nuttall sparrows, of this region at least, includes no "fat" period.

This striking difference between the migratory and nonmigratory populations leads us to suspect a difference in the endocrine systems which may be responsible for the differences in gonad cycle, in prenuptial molt, and in the fat cycle.

FIRST DEPARTURE FROM BERKELEY

There is also an annual variation in the time of first departure from Berkeley. The average testis volume of birds which have completed the molt and have laid on sufficient fat to be classed as fat or very fat is 4.88 mm.[3] As discussed

TABLE 19

First Berkeley Pugetensis Ready for Spring Migration

Year	First Bird with Testis over 4.88 mm.[3]	Average Volume of 3.33 mm.[3]
1936...................	March 7	....
1938...................	March 20	March 17 (interpolated)
1935...................	March 20	March 20
1937...................	March 25	March 24 (interpolated)

above (p. 82), I assume that any bird with testis volume of this size is on the verge of departure. Here again, if we range the years according to dates when first bird with testis volume of 4.88 mm.[3] or over was collected, we find that, except for the fact that 1938 was identical with 1935, the years fall in the same order as for Stage 5 in *nuttalli,* that is, from earliest to latest, 1936, 1938 and 1935, 1937. If we make the average testis volumes comparable by interpolation, we find that a volume of 3.33 mm.[3], reached in 1935 by March 20, would have been reached by March 17 in 1938, but not until March 24 in 1937. Here again, these years fall in the same order as for Stage 5 in *nuttalli,* which is the point in development most nearly comparable to that reached by *pugetensis* at time of departure.

It will be noted that the difference between 1936 and 1937 is of about the same order of magnitude (18 days) as the difference in dates when the average testis volumes reached 2 mm.[3] (16 days) (see p. 88); 1938, however, although still in the right order, falls later than would be expected from the date of average volume of 2 mm.[3] This is obviously due to the retarding effect of the severe conditions of temperature and precipitation in March, as described in the discussion of the late stages of *nuttalli.*

DATE WHEN THE MAJORITY OF PUGETENSIS ARE READY TO DEPART

For 1937 and 1938 I have the dates when the majority of birds collected were ready to depart—that is, had completed the molt, laid on fat, and attained Stage 4 or 5. On March 27, 1938, six out of seven birds had completed the molt and five out of seven had laid on a large amount of fat. The average testis

volume was 4.04 mm.³ On April 3, 1937, four out of five birds had completed the molt and laid on fat. The average testis volume was 4.29 mm.³ To make this comparable to 1938 I interpolated and found that an average volume of 4.04 mm.³ would have been reached by March 31, only three days later than in 1938. This substantiates the small five-day difference between these same years in the dates when the first birds ready to migrate were collected.

The material for 1935 is not so complete, but, if we assume that the bird collected April 7 represents the status of the population as a whole, we may find by interpolation that a volume of 4.04 mm.³ would have been reached by March 31, on identically the same day as in 1937, as was to be expected.

TABLE 20

MAGNITUDES OF ANNUAL DIFFERENCES IN STAGES OF TESTIS DEVELOPMENT
PUGETENSIS AND NUTTALLI

Stage	Differences (in Days) in Testis Development					
	Between 1936 and 1938	Between 1936 and 1935	Between 1936 and 1937	Between 1938 and 1935	Between 1938 and 1937	Between 1935 and 1937
First *pugetensis* taken with testis volume of 4.88 mm.³........	13 days	13 days	18 days	Identical	5 days	5 days
Pugetensis averaging 3.33 mm.³ in testis volume............	......	......	......	3 days	3 days	Identical
Attainment of Stage 5 in *nuttalli*..........	15 days	27 days	34 days	12 days	19 days	7 days

To summarize: All the years for which there is adequate material for the date when the Puget Sound sparrows were ready for departure, when ranged from earliest to latest, fall into the same order as for the date of attainment of Stage 5 in *nuttalli*. But the magnitude of the differences between the years is much less. The difference in earliest departure times for *pugetensis* between 1936 and 1937, for example, is only 18 days as opposed to the 34-day difference in Stage 5 in *nuttalli* for these same years. The difference in earliest departure time between 1938 and 1937 is only 5 to 7 days, whereas the difference between the same years for Stage 5 in *nuttalli* is 19 days. The same climatic conditions produced qualitatively similar effects but of about half the order of magnitude. The relative magnitudes of differences between the two races are summarized in table 20.

ARRIVAL ON THE BREEDING GROUNDS

In spite of the variation in departure time, the main wave of migrants reached Friday Harbor on almost identical dates in 1936, 1937, and 1938. In 1936 the main influx occurred on April 10. A few birds had come earlier, and some came a few days later; but by far the greater proportion of the breeding population arrived in a body. In 1937 Mrs. Fuller reported that the majority of the birds arrived April 9 and 10. Among these were four of the same birds color-banded in 1936, which had arrived on April 10 of that year. In 1938

Mrs. Fuller reported that the majority arrived April 6, including one of the color-banded birds which had arrived on April 10 in 1936. The phenomenon of the arrival is so spectacular that no error in observation is likely.

<div align="center">MEDIAN DATE OF FIRST EGG</div>

Unfortunately, I spent only one spring at Friday Harbor and so have no personal observations of median date for first egg for more than one year. As I have already said, however, through the kindness of Mrs. Fuller I have the date for the first egg in 1937 for one of the identical pairs observed and banded in 1936. The date is only six days later for 1937. In 1936 the female of this pair laid her first egg only two days off the median date for the population, so there is a good chance that the median date is well indicated in 1937 by this single pair. There is a much greater difference between these same years in the dates for first eggs of one of my banded pairs of Nuttalls. In 1936 the female laid her first egg on March 12, whereas in 1937 she laid it on April 13, 34 days later. The median dates for these two years were March 11 and April 13, respectively.

<div align="center">CLIMATIC CORRELATES OF THE GONAD CYCLE OF PUGETENSIS
BERKELEY</div>

Location of the critical period for pugetensis.—In two such closely related populations as *nuttalli* and *pugetensis*, with gonad cycles identical as far as the histology of the stages is concerned, it is very likely, unless the pattern of the cycle is distorted to an improbable degree, that the periods when testis development is most susceptible to climatic conditions roughly coincide; therefore, the critical period in *pugetensis* comprises the time from beginning of recrudescence to Stage 5. Now in the Berkeley Puget Sound sparrows recrudescence, as indicated by the dates when the last testes in inactive condition were taken in 1934 and when the last testes of minimum volume were taken in all four years, did not begin, on the average, before the last week in January. The first bird physiologically ready to depart (the nearest we can come to date of Stage 5 in *pugetensis*) was taken from March 7 to 25, depending upon the year. Therefore, if the analogy with *nuttalli* is justified, the critical period would begin in late January and continue until early to late March at least.

Annual variations in Stage 4 and earliest departure: climatic correlates.— Although the annual variations in Stage 4 and time of earliest departure for *pugetensis* are much less marked than the variations of Stage 5 for *nuttalli*, the contrast between 1936 and the other years is sufficiently great to lead us to expect correlative variations in one or more external factors. Using the method described in the previous section, I ranged the years from earliest to latest dates of Stage 4 and earliest departure, that is (1) 1936, (2) 1938 and 1935, and (3) 1937; I then sought correlative differences in mean temperature, precipitation, and sunshine.

Climatic correlates: mean temperature.—As was to be expected from the results described in the preceding section, correlations with mean temperature were found for all years between December 21 and February 14; that is,

the order of weeks and groups of weeks of corresponding date from warmest to coldest paralleled the order of earliest to latest dates of attainment of Stage 4 and departure. The two- and three-week periods correlated continuously from December 21 to January 31, the four-week periods from December 21 to February 14, and five out of eight of the one-week periods correlated. From February 15 on, the continuous week-to-week correlations ceased, although in 1936 the mean temperature for the three-week period from February 15 to March 7, the date of earliest departure in that year, was higher than that for the same period for the other three years.

It must be understood that this correlation does not contradict what has been said to the effect that the period beyond January 31 does not correlate for *nuttalli* since for *pugetensis* the year 1934, which would probably cause the correlation to stop at January 31, is not included.

Climatic correlates: precipitation.—The same method produced no correlations with precipitation. The weeks and groups of weeks always failed to parallel the order of years for Stage 4 and earliest departure.

Climatic correlates: sunshine.—Only three one-week periods, one of two weeks, and one of three weeks correlated with the order of the years from earliest to latest. These correlations are discontinuous and ill distributed and provide inadequate evidence of any primary connection.

Slightness of annual variation in both gonad cycle and climatic factors.— If we are approximately correct in our location of the critical period of *pugetensis,* the reason for the slightness of annual variation in the gonad cycle is plain. Since the critical period of *pugetensis* begins much later than does that of *nuttalli,* only the earliest part falls during the period when mean temperature in central California shows a high annual variation. Most of it falls not only at the season when conditions are becoming more equable for any one year but also when the temperature conditions of the four years in question tend to converge. For example, from December 21 to January 31 the weekly mean temperature of 1936 averaged 2.7°–11.8° higher than that of 1937. From February 1 on, the weekly mean of 1936 averaged from .5° colder to 5.1° warmer. Thus, although 1936 continued on the average to be warmer than 1937, the difference between the two years decreased materially.

Thus it was to be expected, on the basis of the relative positions of the period of high annual variation in mean temperature and of the critical period of *pugetensis,* that the effect of the early wide annual variations in temperature with which the testis development of *nuttalli* accords so accurately would not be reflected to a similar degree in the identical stages of testis development in *pugetensis;* and this I have already shown to be so.

FRIDAY HARBOR

From the daily data charted in figure 13 I calculated the weekly mean temperature and weekly totals of precipitation for Friday Harbor in 1936 for the period beginning February 25, about six weeks before the main influx of the birds, and ending with May 11, when all the first eggs had been laid. The most outstanding fact is that the median date for copulation comes two weeks

after a sudden upswing in the weekly mean temperature from 41.4° to 48.7° and just one week after the mean temperature passed 50°, above which it stayed for the remainder of the breeding season. The precipitation and snowfall show a decrease with the upswing of the temperature, although the change is not so striking. As far as nesting was concerned, the birds were ready as soon as, or before, the conditions were favorable. Many began to build nests before the trees were leafed out, but the leaf growth was so sudden and rapid that, by the time the eggs were laid, the foliage was sufficient to hide the nests.

Although there would be great variation from year to year, causing acceleration or delay after arrival, the situation in 1936 was probably about typical. The birds, working to northward, reach their breeding grounds about the time the steep gradient of the breeding-ground climate approximates the conditions left behind in the far more equable climate of the wintering grounds.

DISCUSSION

For *pugetensis,* probably owing to the equability of the later season, it is possible to discuss the cycle in terms of date as well as of histological stage since, with the exception of 1936, the dates of the stages are approximately the same from year to year.

The greater part of the physiological preparation does not take place on the breeding grounds. The beginning and early stages occur on the wintering grounds, evidently affected by the conditions within a critical period which, in the average year, seems wholly or partly to follow January 25, but which cannot be shown to be critical after mid-February. Presumably owing to the equability of the March climate, it is impossible in *pugetensis* to define the latter limits of the critical period by the annual variations of the testis stages. Only in the warmest year, 1936, does the first testis over 4.88 mm.[3]—between Stages 4 and 5 (most birds migrate before Stage 5 is reached)—vary from the norm, antedating the three other years by 13 to 18 days. Correspondingly, of course, the duration of the critical period cannot be suggested by the climatic correlates beyond mid-February, when the more equable spring climate ceases to show substantial annual variations.

As has already been suggested, it seems probable, considering the closeness of the races and the qualitative identity of testis development with respect to histology (though not as to date or rate), that the period of susceptibility to external conditions would fall between like histological limits, that is, between Stages 2 and 5 or between late January and late March. Hence, in all probability, under average conditions any annual variation which exists between breeding dates at the far northern stations is determined by conditions on the wintering grounds, perhaps a thousand miles to the southward, and a month or two before.

The bulk of the male development is divided more or less evenly between the flight north and the ensuing ten days on the breeding grounds. Probably, by analogy with *nuttalli,* this stage of development is apt to be almost mechanically regular, like a clock once wound up. It might, however, bear a complex relationship to the conditions of the zones passed through, just as the culmina-

tion of the cycle was modified by phenomenal conditions on the threshold of the nesting season of *nuttalli* in Berkeley in 1938. It is extremely probable, however, that the main testicular enlargement during migration usually runs its course, little influenced by the zones and conditions to which the bird is exposed. We can at least say that neither the long flight nor the northern zones traversed are essential to full development since this was attained by the incapacitated bird which remained in Berkeley (see p. 41). And actually, although the more northern zones might show more annual variation at this time, there is surprisingly small average difference between the conditions left on the wintering grounds and those found a thousand miles to northward. The weekly averages for the period are of similar orders of magnitude, and even the differences in the condition of the flora are far less great than would be expected. T. T. McCabe, in a rapid trip north in mid-April, 1937, kept a careful record of the states of a score of flowering plants on similar altitudes and exposures along the coast between northern California and Vancouver, B.C., and found an almost complete absence of latitudinal succession. Similar plants were in a similar stage of flower in the environs of Eureka and Vancouver within four days of the same date.

Annual Regulation of Migration

It is implicit in what has already been said of the condition of the birds just previous to departure from Berkeley, that migration occurs in strict correlation with a complex and deep-seated physiological development which has been proceeding in its various manifestations for a long time and which has been shown to be in some degree controlled by remote climatic conditions. Testis change has been in progress at least eight weeks, molt for about four weeks, and the accumulation of fat for six weeks. It is logical to conclude from the constancy of these correlative conditions that migration is not a last-moment effect of contemporaneous or nearly contemporaneous climatic conditions but rather fits into its place in the grand pattern as inevitably as a single element of a picture puzzle. I have been able to describe only two or three of the more obvious elements of the pattern. Of the more deep-seated physiological controls we know nothing.

It is impossible, therefore, to say with Kendeigh (1934) that spring migration is regulated and timed by rising temperatures and increasing daily periods of light, because migration is obviously a tightly bound-in element of a complex process, genetically fixed or annually variable in response to circumstances of greater remoteness in time and longer duration than such a concept would imply.

A, precipitation, in inches; B, mean relative humidity (per cent); C, percentage of possible hours of sunshine; D, curve of variation in hours of daylight from beginning of twilight to end of twilight (minimum, 12 hours, 43 minutes; maximum, 18 hours, 43 minutes; two spaces represent one hour of increase or decrease); E, temperature (degrees Fahrenheit): continuous line, daily mean; broken line, daily maximum; F, volumes of testes in cubic millimeters: small dots represent developing testes of less than 4 mm.³, large dots represent testes of over 4 mm.³, one space $=$ 4 mm.³; G, behavior: (1) first egg, $\bullet$ $=$ seen, $\bigcirc$ $=$ calculated; (2) nest begun, $\smile$ $=$ seen, $\smile$ $=$ calculated; (3) first copulation; (4) trilling and posturing ($\female$); (5) chasing and fighting ($\male$); (6) song ($\male$).
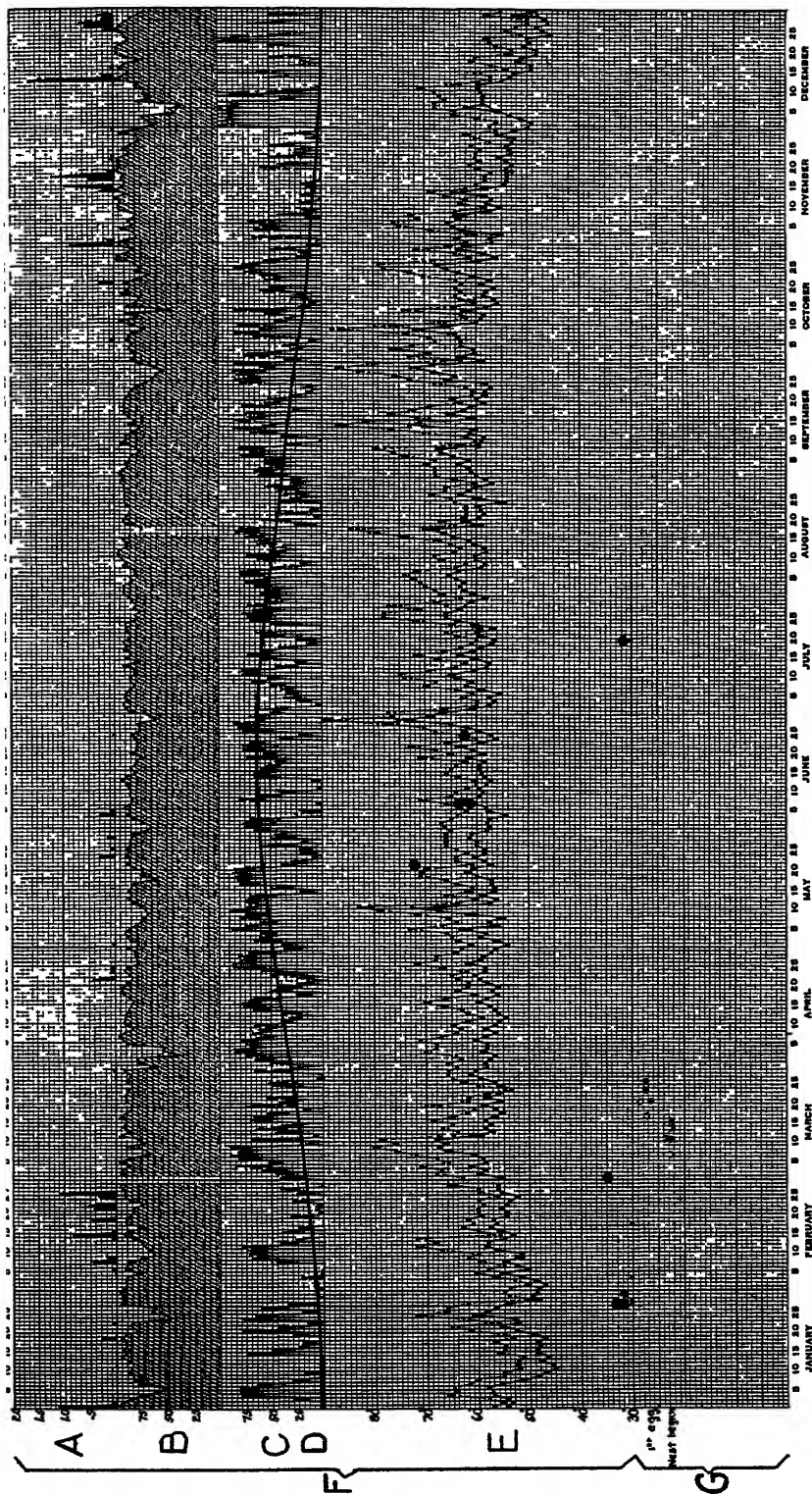
Fig. 8

Berkeley, 1934.
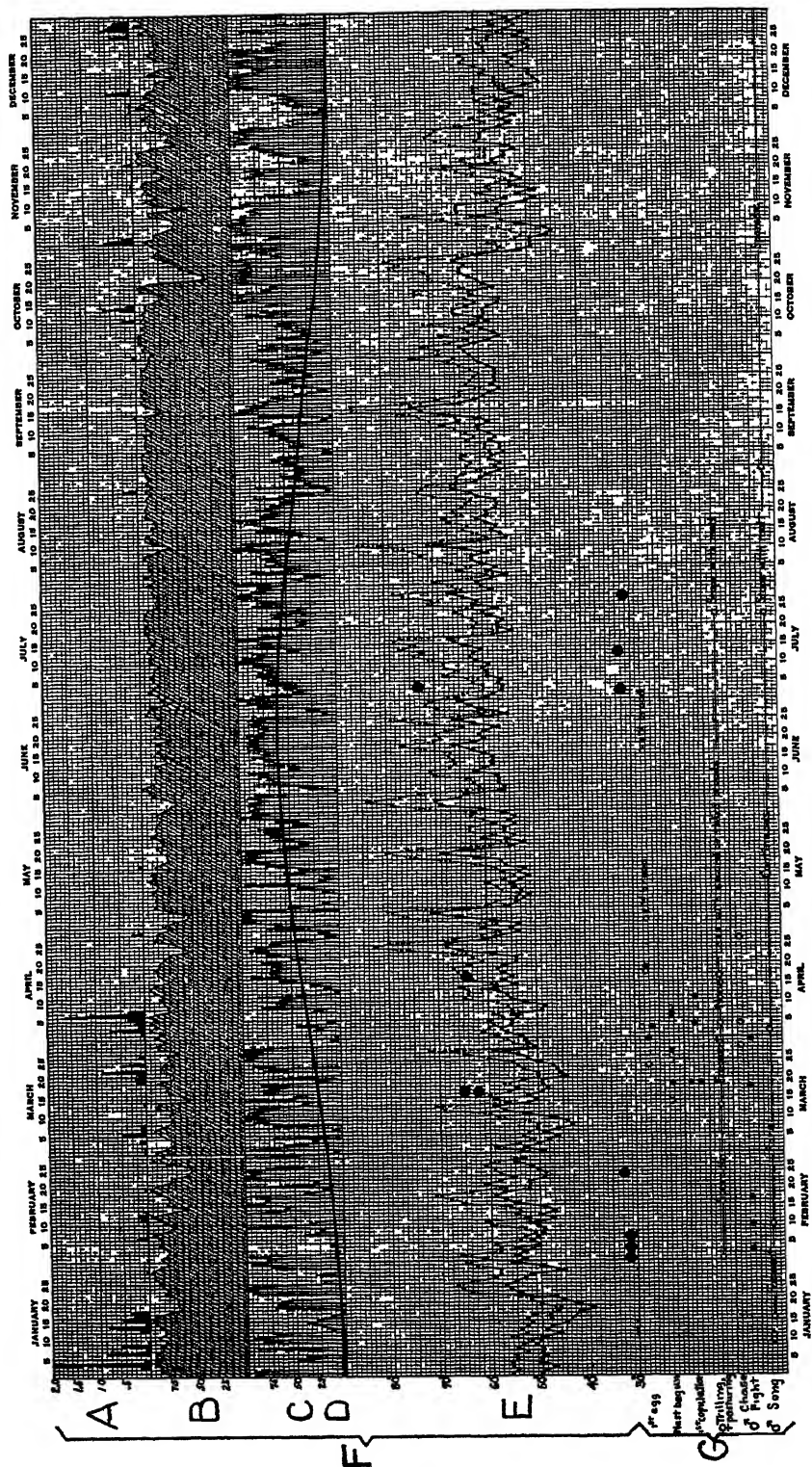
Fig. 9
Berkeley, 1935.
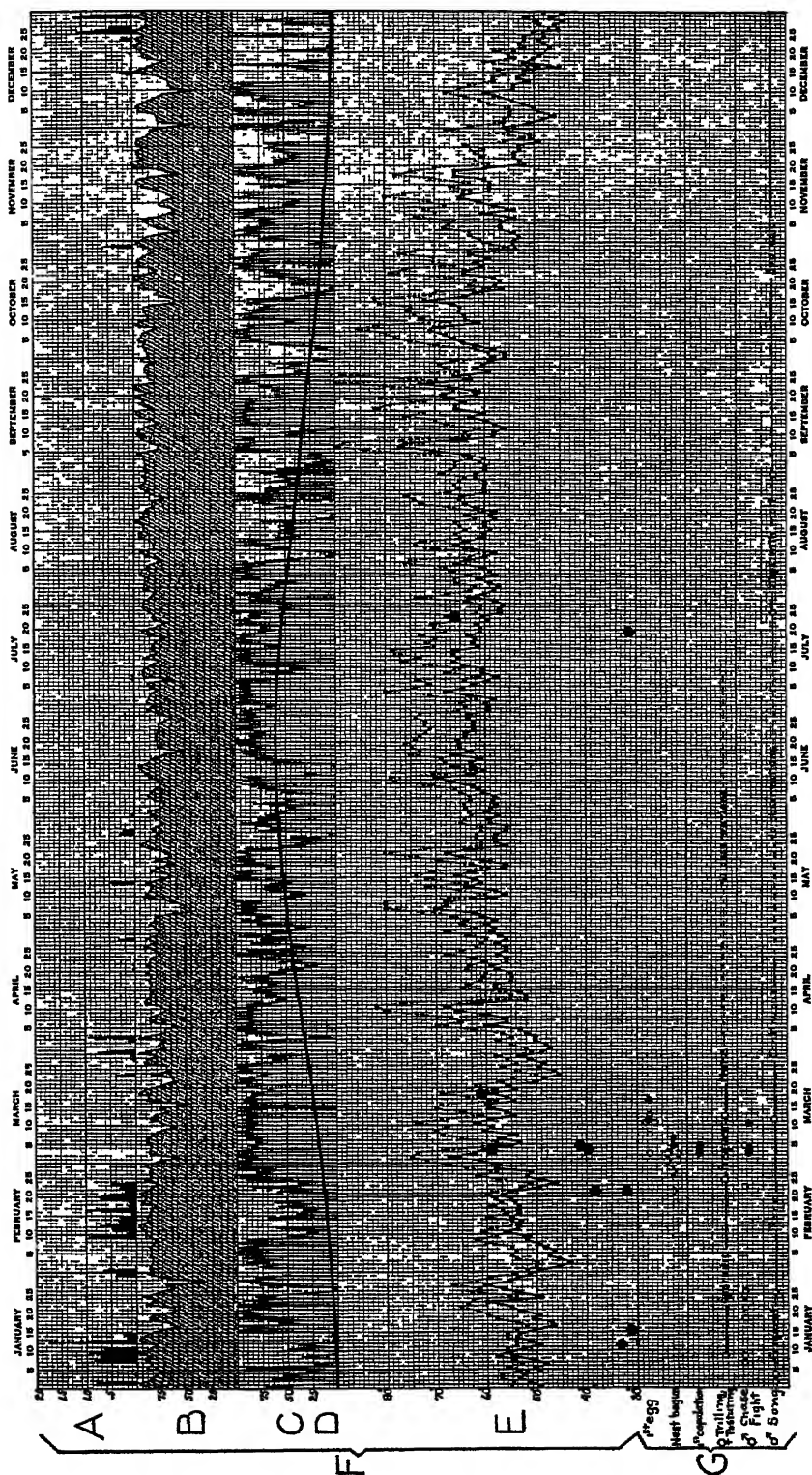
Fig. 10

Berkeley, 1936.

[99]
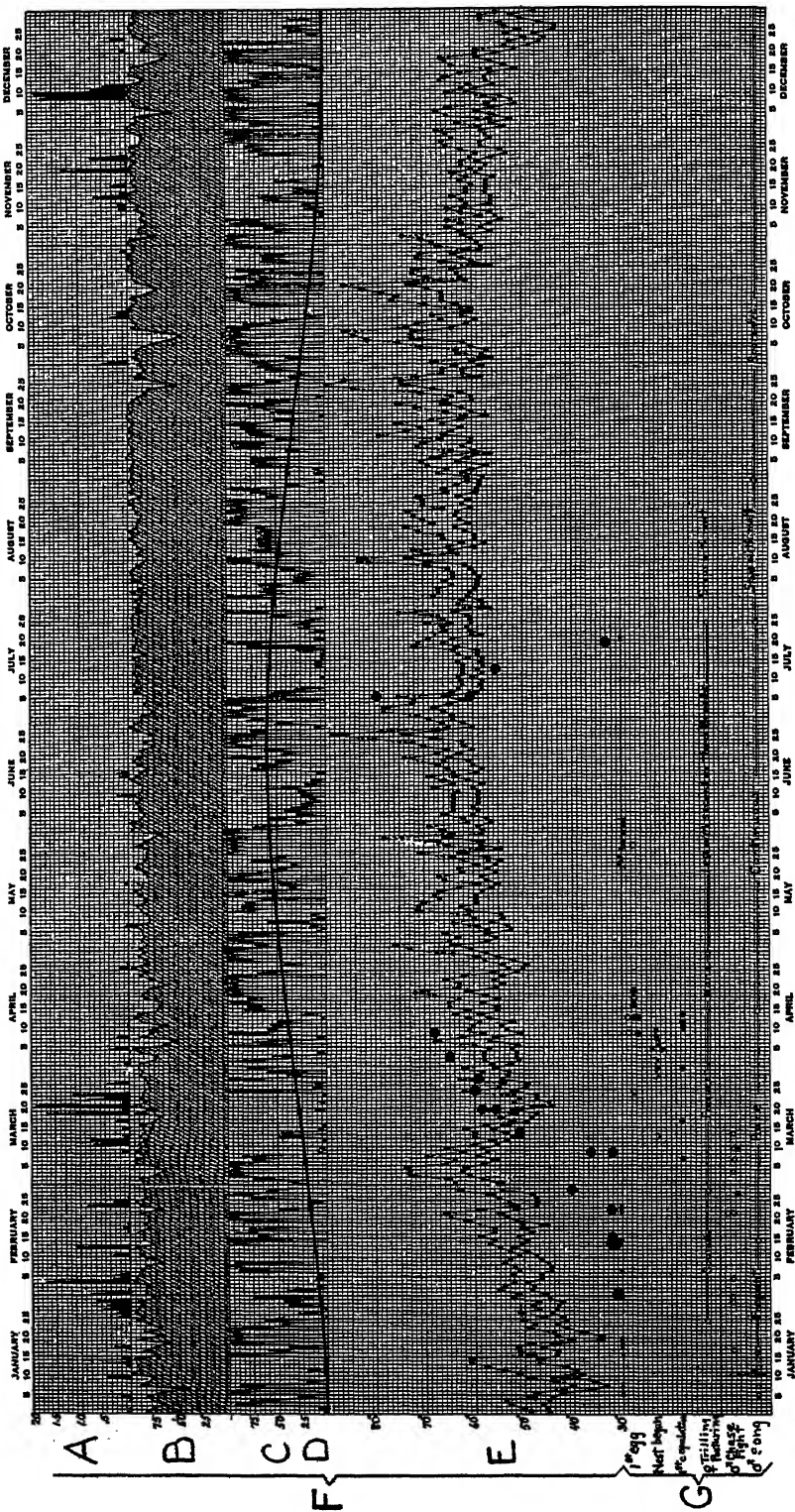
Fig. 11
Berkeley, 1937.
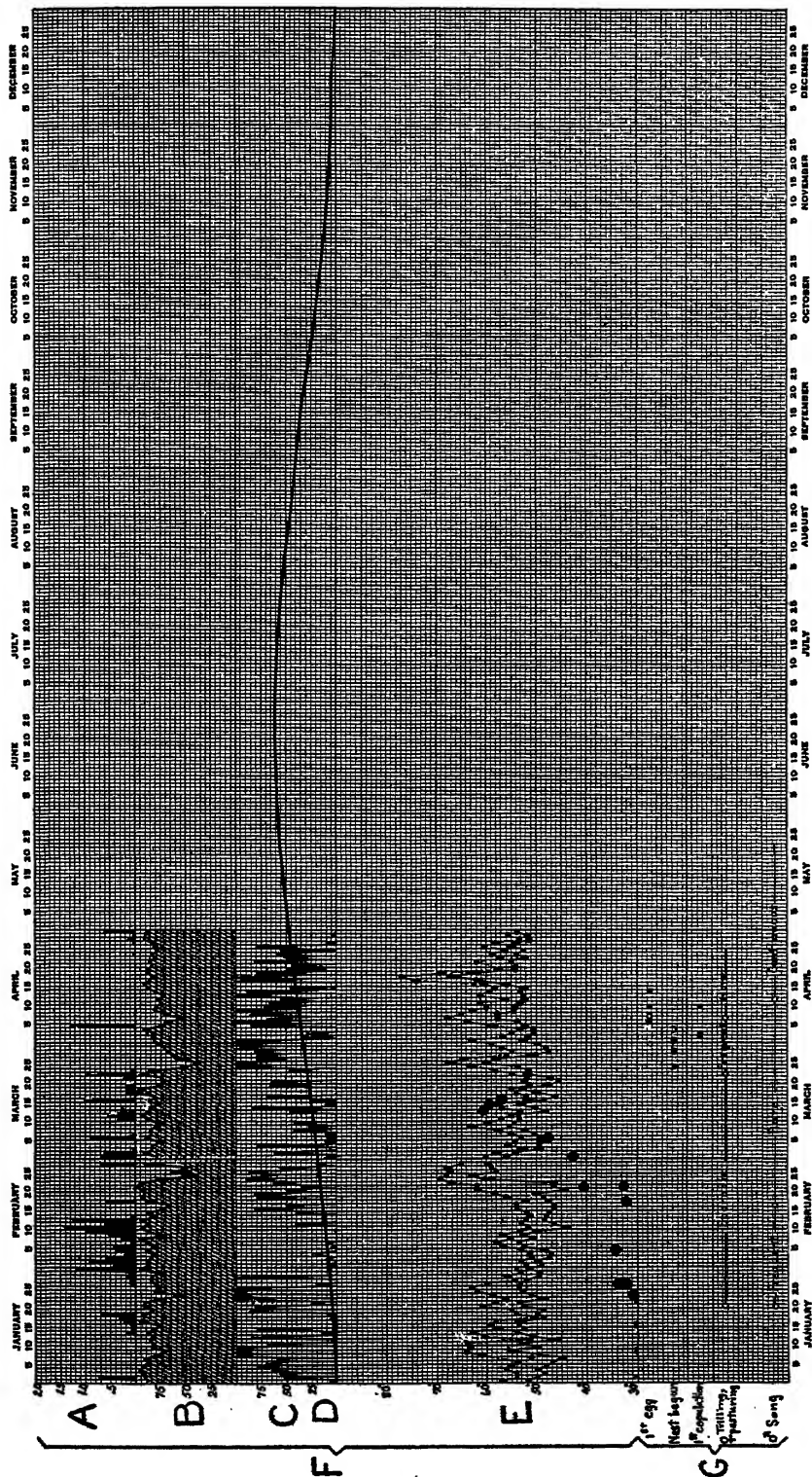
Fig. 12
Berkeley, 1938.
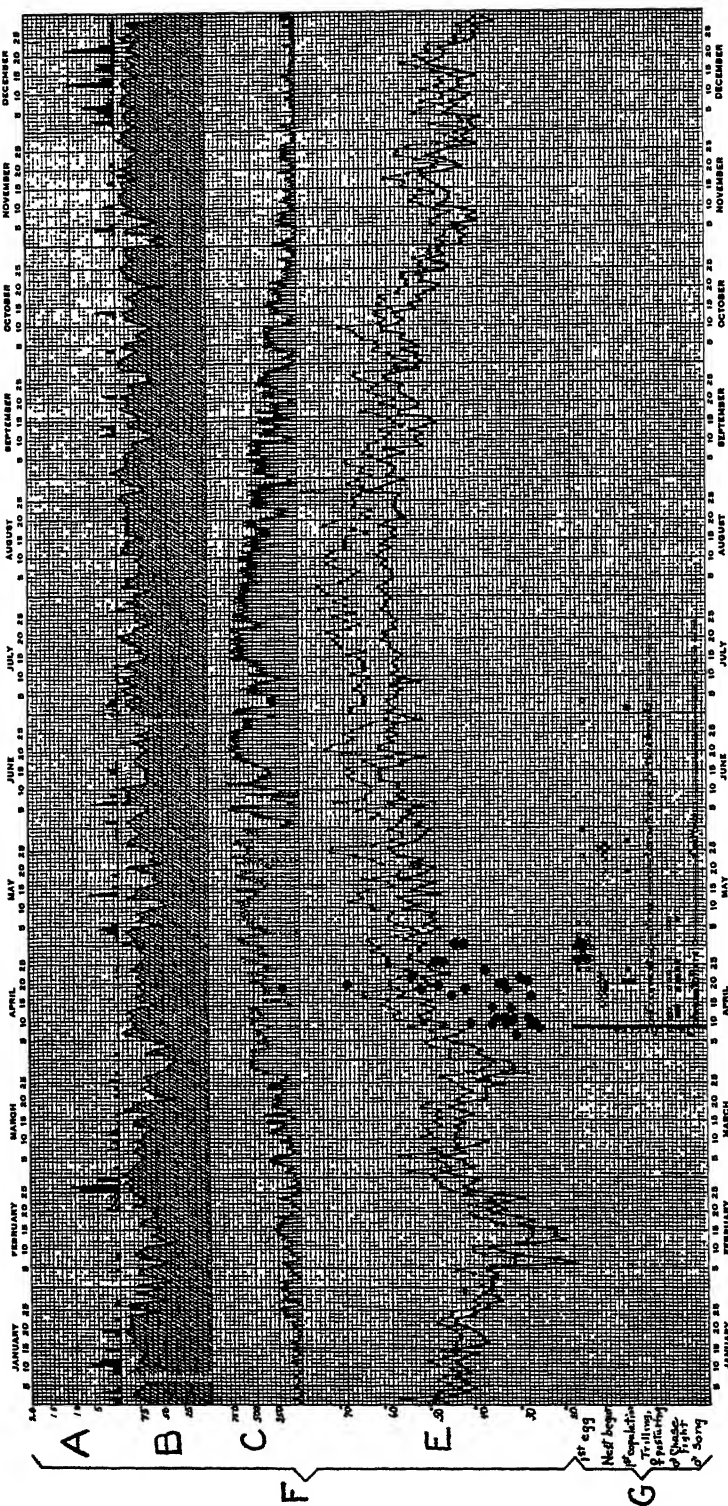
Fig. 13

Friday Harbor, 1936.

A, precipitation, in inches (s = snow); B, relative humidity (per cent); C, solar radiation, in calories per square centimeter; E, temperature (degree Fahrenheit), continuous line, daily mean; broken line, daily maximum; F, volumes of testes in cubic millimeters (1 space = 4 mm.³); G, behavior: (1 first egg, ● = seen, ○ = calculated; (2) nest begun; (3) first copulation; (4) trilling and posturing (♀); (5) chasing and fightin (♂); (6) song (♂).

Fig. 14

Behavior and testis development, 1936: *nuttalli* (Berkeley) and *pugetensis* (Berkeley, Friday Harbor, and Victoria).

Early stages of the testis: *nuttalli*.

△ = inactive condition.

▭ = Stage 2.

▯ = Stage 3.

▢ = Stage 4.

◯ = Stage 5.

2 spaces on horizontal scale = one day.

10 spaces on vertical scale = 1 m.^{3} testis volume.

Solid symbols, sectioned; hollow symbols, estimated from volume.
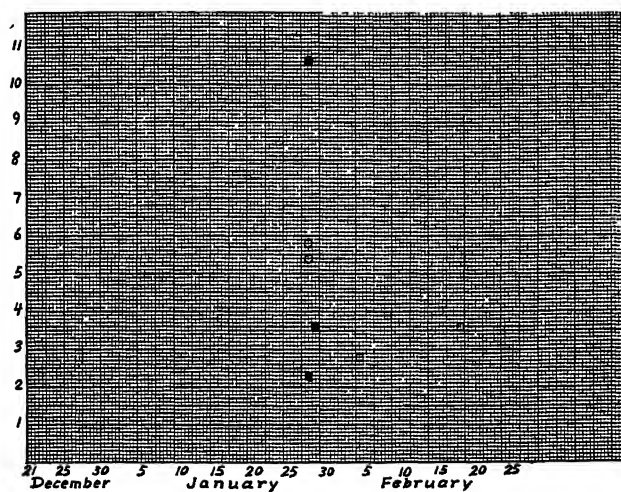
Fig. 15

1933–34
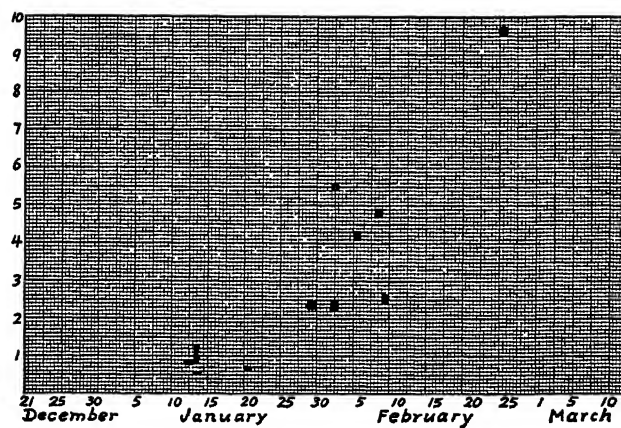
Fig. 16

1934–35
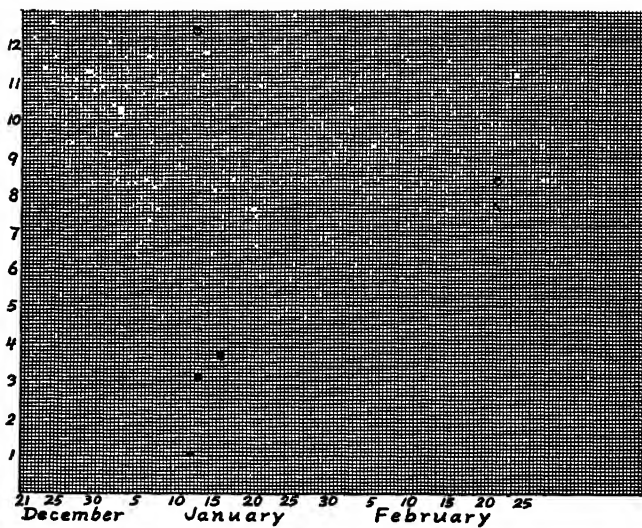
Fig. 17
1935–36
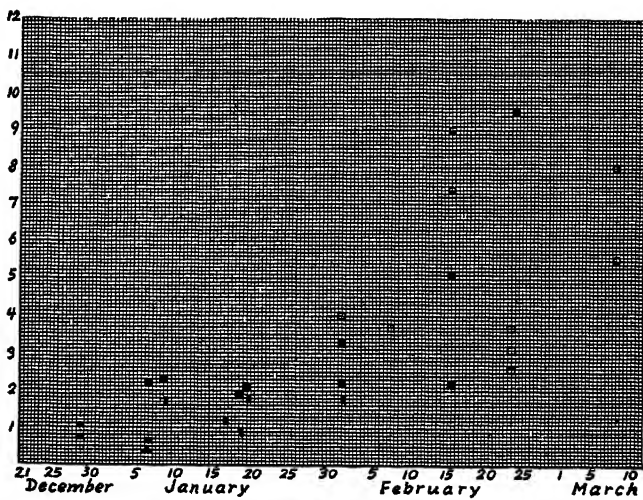
Fig. 18
1936–37

Fig. 19
1937–38

Figs. 20–24
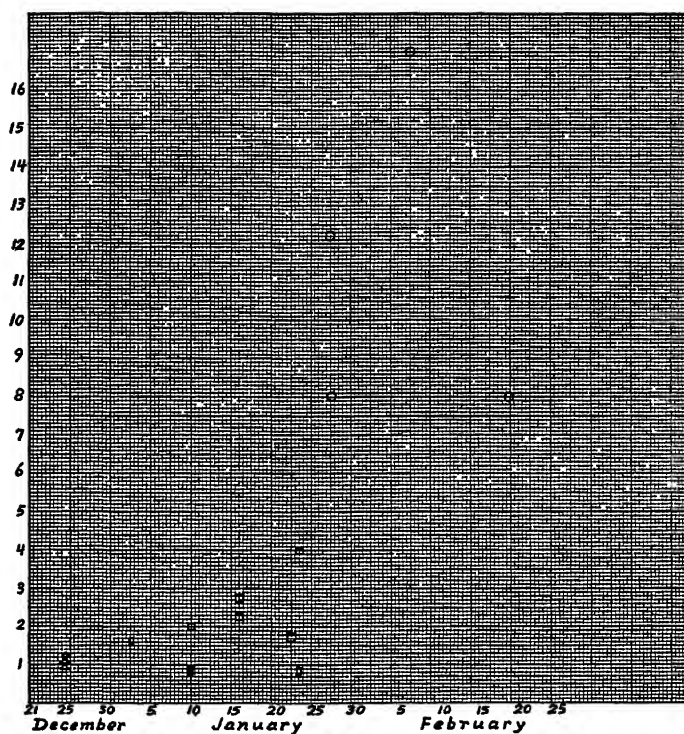
Early stages of the testis: wintering *pugetensis* at Berkeley.

$\triangle$ = inactive condition.

▭ = Stage 2.

▯ = Stage 3.

▢ = Stage 4.

○ = Stage 5.

2 spaces on horizontal scale = one day.

10 spaces on vertical scale = 1 m.³ testis volume.

Solid symbols, sectioned; hollow symbols, estimated from volume.
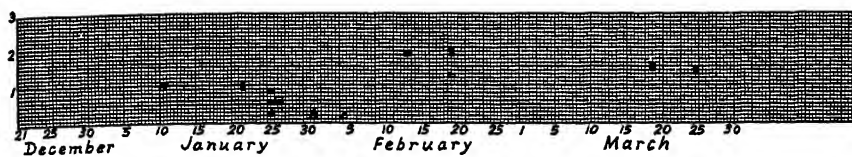
Fig. 20
1933-34
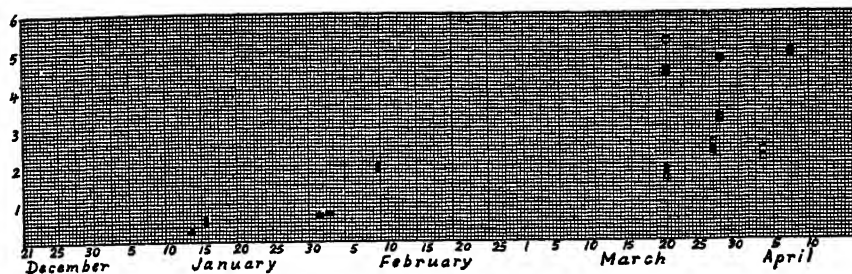
Fig. 21
1934-35
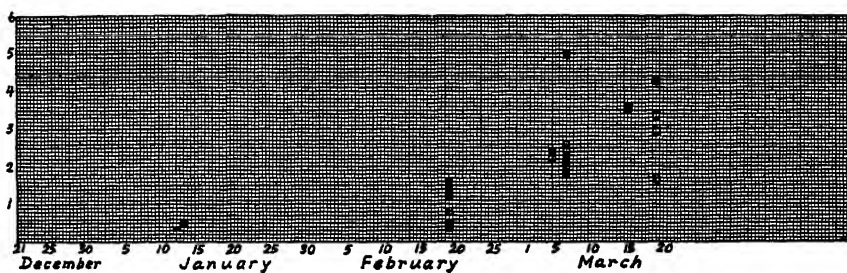
Fig. 22
1935-36
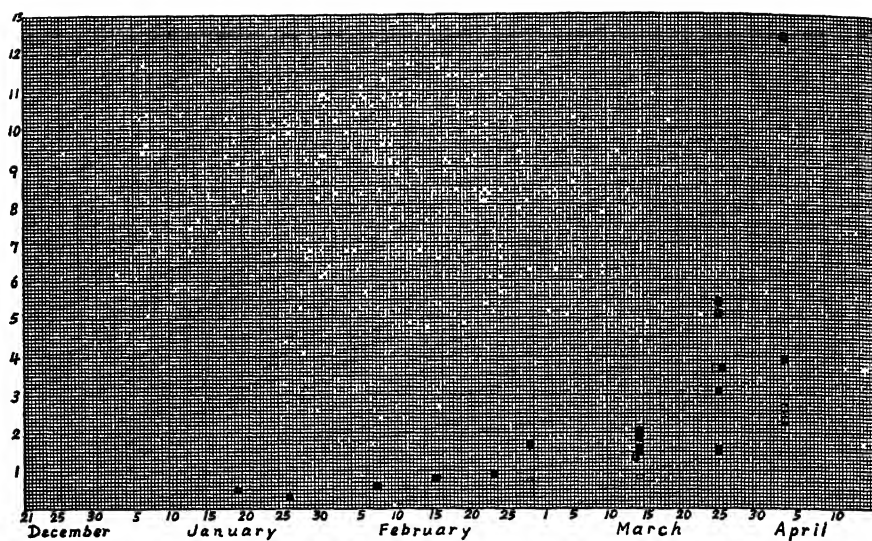
Fig. 23
1936–37
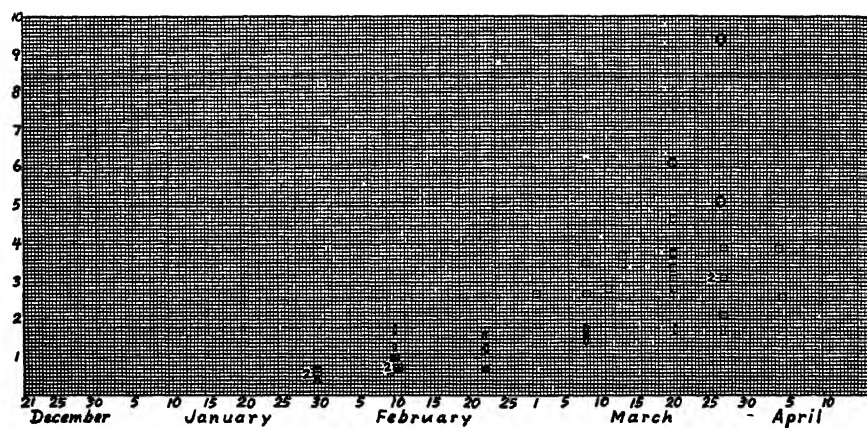
Fig. 24
1937–38
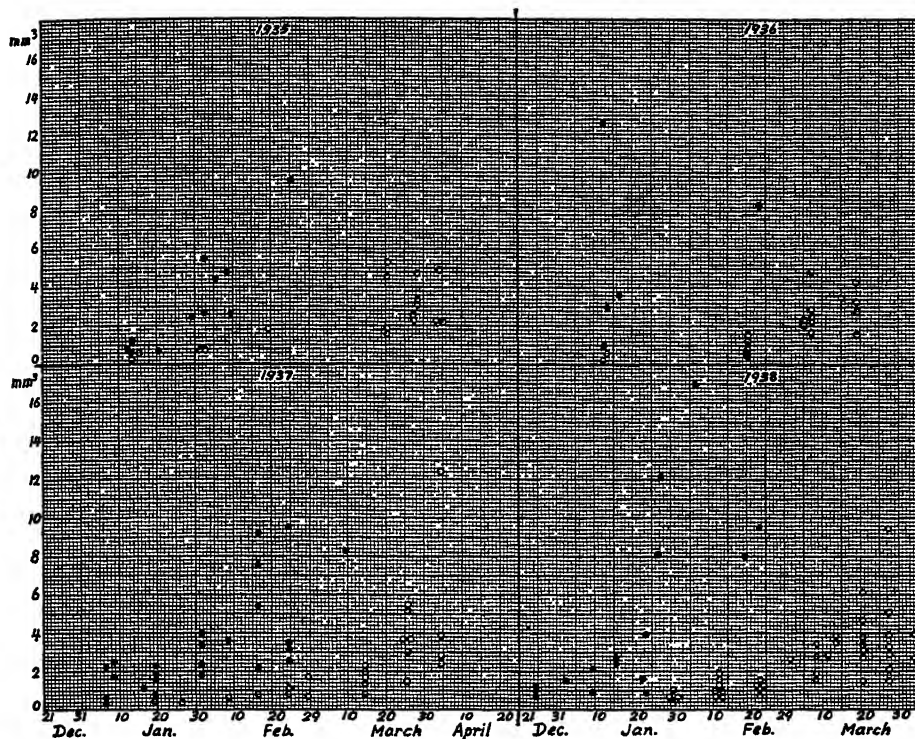
Fig. 25. Early stages of the testis at Berkeley, *nuttalli* (●) and *pugetensis* (○).
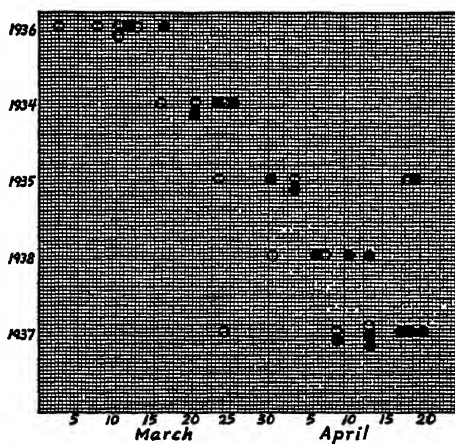
Fig. 26

First eggs: *nuttalli*, seen (●) and calculated (○).
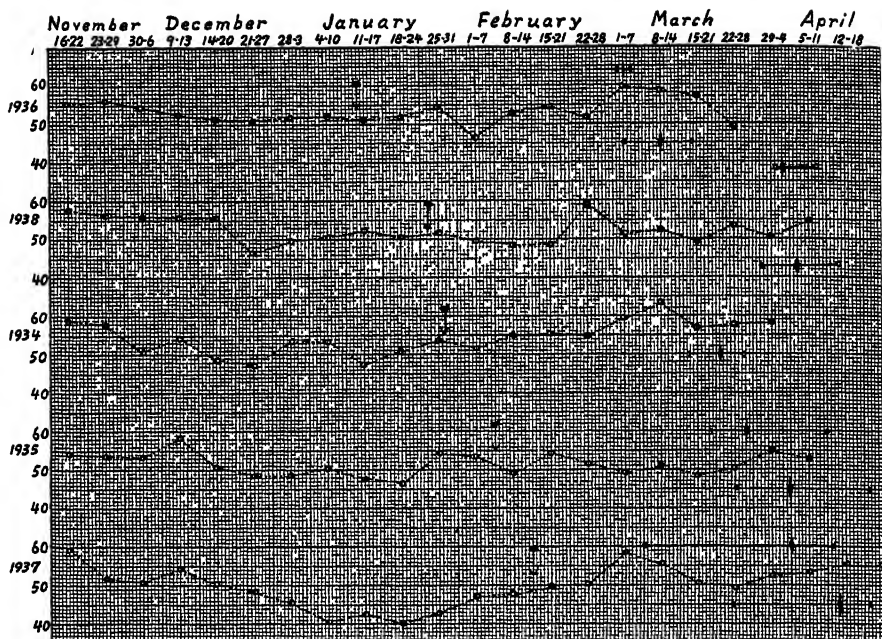
Fig. 27

Weekly mean temperature at Berkeley.

↓ = date Stage 5.

○——◆——○ below = first eggs, with median date.

○——◆——○ above = first copulations, with median date.

Figures on vertical scale indicate degrees Fahrenheit.
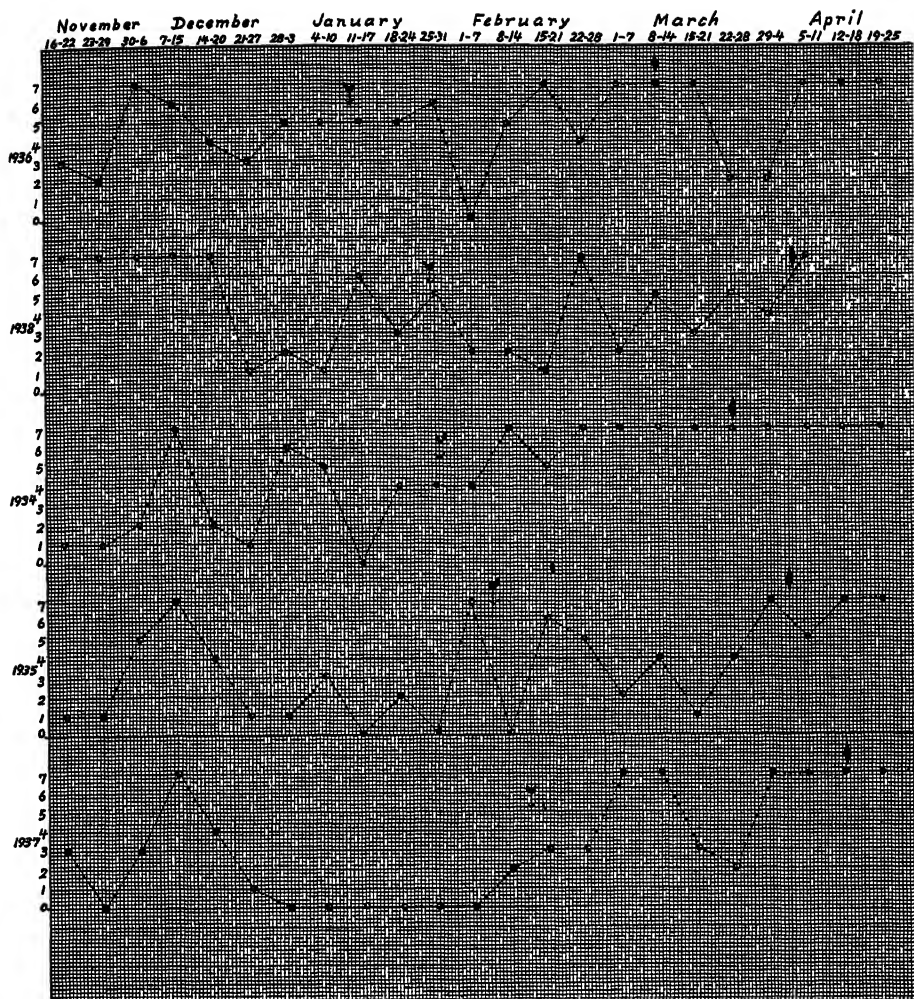
Fig. 28

Number of days mean daily temperature
above 50° F. at Berkeley.

↓ = date Stage 5.
◆ = median date first eggs.

[113]
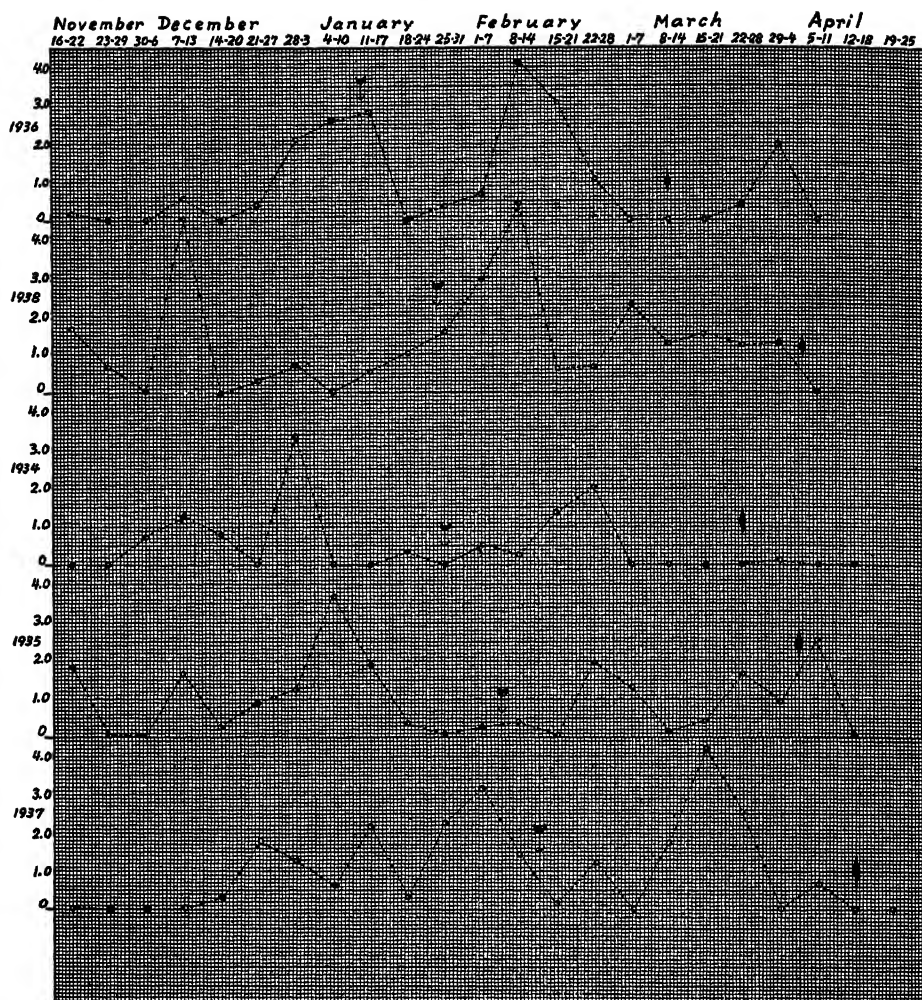
Fig. 29

Weekly totals of precipitation at Berkeley.

↓ = date Stage 5.

◆ = median date first eggs.
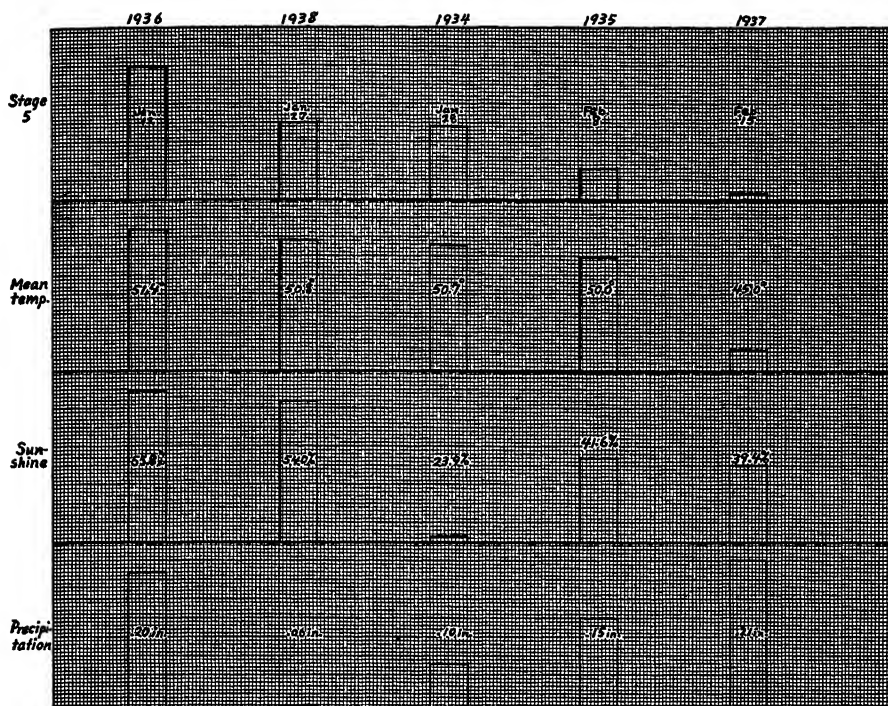
Fig. 30

Date of Stage 5 and magnitude of averages of mean temperature and sunshine and of totals
of precipitation for the duration of Period II at Berkeley for five years.

APPENDIX I

Measurements and Weights

TABLE 1
Breeding Males
(Length of right wing in millimeters)

Locality	Number	Mean	σm	Extremes	σ	σσ	V
West-central California..........	21	71.63	0.35	67.4–74.2	1.62	0.25	2.26
Humboldt and Del Norte counties	30	71.59	.27	68 8–74.5	1.50	.19	2.09
Tillamook and Netarts, Oregon...	11	71.70	.41	69.7–74.0	1.37	.28	....
Friday Harbor, Washington......	34	71.55	.29	67.4–74.3	1.70	.21	2.38
Washington mainland and Vancouver, B. C..................	12	69.21	.46	67.7–73.4	1.57	.32	....
Vancouver Island................	39	72.21	0.29	68.4–76.4	1.78	0.20	2.46

TABLE 2
Breeding Females
(Length of right wing in millimeters)

Locality	Number	Mean	σm	Extremes	σ	σσ	V
West-central California..........	20	67.99	0.37	65.3–71.7	1.63	0.26	2.40
Humboldt and Del Norte counties	11	66.72	.42	64.3–68.8	1.38	.30	....
Tillamook and Netarts, Oregon...	10	68.66	.40	67.2–70.8	1.27	.28	....
Friday Harbor, Washington......	11	67.79	.44	65.0–69.7	1.47	.31	....
Washington mainland and Vancouver, B. C..................	7	66.96	.27	65.5–67.9	0.72	.19	....
Vancouver Island................	14	68.46	0.37	66.4–71.5	1.37	0.26	....

TABLE 3
Breeding Males
(Length of tail in millimeters)

Locality	Number	Mean	σm	Extremes	σ	σσ	V
West-central California..........	16	69.93	0.48	67.3–74.4	1.93	0.34	2.76
Humboldt and Del Norte counties	29	69.15	.28	66.0–73.6	1.52	.20	2.20
Tillamook and Netarts, Oregon...	11	69.29	.69	65.5–73.0	2.29	.49	....
Friday Harbor, Washington......	34	69.84	.33	64.6–73.3	1.94	.24	2.77
Washington mainland and Vancouver, B. C..................	12	68.66	.73	63.6–72.2	2.52	.52	....
Vancouver Island................	38	69.93	0.34	65.4–73.9	2.08	0.24	2.97

TABLE 4
BREEDING FEMALES
(Length of tail in millimeters)

Locality	Number	Mean	σm	Extremes	σ	σσ	V
West-central California..........	17	66 55	0.52	63.3–70.1	2.13	0 37	3.20)
Humboldt and Del Norte counties	10	66.37	.72	62.8–69.3	2.27	.51	....
Tillamook and Netarts, Oregon...	10	65 83	.53	63.0–68 3	1.67	.37	....
Friday Harbor, Washington......	11	66.28	.72	63.4–70 3	2.40	.51	....
Washington mainland and Vancouver, B. C....................	6	64.62	.60	63.2–67.0	1.47	.42	....
Vancouver Island................	14	66.62	0.59	62.0–69.5	2.21	0.42	....

TABLE 5
BREEDING MALES
(Length of tarsus in millimeters)

Locality	Number	Mean	σm	Extremes	σ	σσ	V
West-central California.........	27	22.75	0.14	20.7–23.6	0.72	0.10	3.17
Humboldt and Del Norte counties	30	22.39	.15	20.7–24.0	.85	.11	3.78
Tillamook and Netarts, Oregon...	11	21.76	.12	21.1–22.5	.41	.09	....
Friday Harbor, Washington......	34	21.74	.13	20.3–23.5	.75	.09	3.43
Washington mainland and Vancouver, B. C....................	12	21.51	.27	20.2–23.1	.93	.19	....
Vancouver Island................	39	21.66	0.10	20.2–22.8	0.61	0.08	2.80

TABLE 6
BREEDING FEMALES
(Length of tarsus in millimeters)

Locality	Number	Mean	σm	Extremes	σ	σσ	V
West-central California..........	20	22.17	0.15	21.1–23.6	0 67	0.11	3.02
Humboldt and Del Norte counties	11	21.57	.22	20.3–22.4	.74	.16	....
Tillamook and Netarts, Oregon...	10	21.33	.15	20.6–22.1	.47	.11	....
Friday Harbor, Washington......	11	21.24	.22	20.3–22.3	.72	.15	....
Washington mainland and Vancouver, B. C....................	8	21.01	.26	20.3–22.0	.74	.18	....
Vancouver Island................	14	21.16	0.23	20.0–22.6	0.87	0.16	....

TABLE 7

BREEDING MALES

(Length of middle toe in millimeters)

Locality	Number	Mean	σm	Extremes	σ	σσ	V
West-central California..........	27	17.64	0.15	16.0–18.9	0.75	0.10	4.28
Humboldt and Del Norte counties	30	17.49	.12	16.2–19.0	.68	.09	3.89
Tillamook and Netarts, Oregon...	11	16.69	.22	15.4–17.5	.71	.15	....
Friday Harbor, Washington......	33	17.18	.12	15.4–18.3	.66	.08	3.87
Washington mainland and Vancouver, B. C..................	12	17.19	.22	16.3–18.7	.76	.16	....
Vancouver Island................	39	17.29	0.10	15.9–19.6	0.65	0.07	3.74

TABLE 8

BREEDING FEMALES

(Length of middle toe in millimeters)

Locality	Number	Mean	σm	Extremes	σ	σσ	V
West-central California..........	20	16.98	0.15	15.4–18.2	0.68	0.11	3.99
Humboldt and Del Norte counties	11	17.48	.16	16.4–18.1	.53	.11	....
Tillamook and Netarts, Oregon...	10	16.80	.24	15.8–18.3	.75	.17	....
Friday Harbor, Washington......	10	16.83	.29	15.3–18.2	.93	.21	....
Washington mainland and Vancouver, B. C..................	8	16.39	.20	15.1–16.9	.58	.14	....
Vancouver Island................	14	17.06	0.13	16.4–18.1	0.49	0.09	....

TABLE 9

BREEDING MALES

(Length of bill in millimeters)

Locality	Number	Mean	σm	Extremes	σ	σσ	V
West-central California..........	26	8.37	0.08	7.6–9.2	0.39	00.5	4.63
Humboldt and Del Norte counties	30	8.15	.05	7.5–9.0	.29	.04	3.57
Tillamook and Netarts, Oregon...	11	7.96	.08	7.4–8.4	.28	.06	....
Friday Harbor, Washington......	33	7.76	.50	7.3–8.4	.28	.03	3.64
Washington mainland and Vancouver, B. C..................	12	8.08	.10	7.5–8.5	.34	.07	....
Vancouver Island................	39	8.03	0.05	7.4–8.9	0.33	0.04	4.10

TABLE 10

BREEDING FEMALES

(Length of bill in millimeters)

Locality	Number	Mean	σm	Extremes	σ	σσ	V
West-central California..........	21	8.12	0.06	7.5–8.7	0.29	0.04	3.53
Humboldt and Del Norte counties	10	8.07	.08	7.6–8.4	.25	.06	....
Tillamook and Netarts, Oregon...	10	7.85	.12	7.4–8.4	.37	.08	....
Friday Harbor, Washington......	10	7.87	.08	7.5–8.2	.25	.06	....
Washington mainland and Van-couver, B. C...................	8	7.85	.08	7.6–8.2	.23	.06	....
Vancouver Island................	14	7.99	0.12	7.1–8.9	0.45	0.09	....

TABLE 11

BREEDING MALES

(Ratios of sixth primary to fifth secondary)

Race	Length, 6th primary		Length, 5th secondary		Ratio, 6th primary to 5th secondary	
	No.	Mean	Extremes	Mean	Extremes	Mean	Extremes
nuttalli...............	15	57.74	55.5–60.2	48.35	46.0–51.6	1.19	1.13–1.24
pugetensis............	15	57.08	54.4–59.3	47.93	45.6–49.7	1.19	1.12–1.24

TABLE 12

WEIGHTS OF MALES AT BERKELEY

Age	Number	Mean, gm.	σm	Extremes	σ	σσ	V
	A. *nuttalli,* breeding						
Adult...........................	17	28.4	0.46	25.9–33.4	1.86	0.32	6.54
Immature.......................	10	27.3	0.29	25.4–28.8	0.92	0.21	....
	B. *nuttalli,* wintering						
Adult...........................	28	29.1	0.47	24.3–33.3	2.49	0.33	8.55
Immature.......................	19	27.7	0.27	24.2–29.7	1.18	0.19	4.28
	C. *pugetensis,* wintering						
Adult...........................	43	26.6	0.36	23.2–29.7	2.32	0.25	8.75
Immature.......................	..	....	....	....	....	....	....

TABLE 13

WEIGHTS OF FEMALES AT BERKELEY

Age	Number	Mean, gm.	σm	Extremes	σ	$\sigma\sigma$	V
	A. *nuttalli*, breeding						
Adult............................	9	26.6	0.28	25.6–28.2	0.83	0.20	....
Immature........................	9	26.3	0.86	21.8–28.3	2.56	0.60	....
	B. *nuttalli*, wintering						
Adult............................	11	26.7	0.49	24.6–29.7	1.63	0.35	....
Immature........................	21	25.6	0.40	21.8–28.3	1.85	0.29	7.25
	C. *pugetensis*, wintering						
Adult............................	13	24.9	0.55	22.1–29.7	1.99	0.39	....
Immature........................	..	....	....	....	....	....	....

APPENDIX II

TABLES OF METEOROLOGICAL DATA FOR BERKELEY

(Graphed in figs. 8–12, 27–29)

TABLE 1
AVERAGE MEAN TEMPERATURE (deg. F.)

Years	Two-week Periods									
	November 23–December 6	December 7–December 20	December 21–January 3	January 4–January 17	January 18–January 31	February 1–February 14	February 15–February 28	March 1–March 14	March 15–March 28	March 29–April 11
1935–1936	55.3	51.8	51.1	51.5	53.1	49.8	53.1	59.3		
1933–1934	54.3	51.5	50.3	50.3	52.4	53.2	55.2	61.2	57.1	
1937–1938	56.1	55.6	48.0	51.3	51.0	49.3	53.9	51.8	51.2	52.4
1934–1935	53.6	54.6	48.5	49.0	50.5	51.4	53.3	50.1	49.7	54.1
1936–1937	51.5	52.4	46.6	41.5	41.6	47.4	50.0	57.3	49.8	53.1

Years	Three-week Periods						
	November 30–December 20	December 21–January 10	January 11–January 31	February 1–February 21	February 22–March 14	March 15–April 4	April 5–April 25
1935–1936	52.7	51.4	52.5	51.3	56.7		
1933–1934	51.2	51.3	50.7	54.0	59.0	57.5	
1937–1938	55.7	48.8	51.3	49.0	54.2	50.8	
1934–1935	54.2	49.0	49.6	52.5	50.6	51.6	
1936–1937	51.9	44.5	42.0	48.2	55.0	50.8	55.0

Years	Four-week Periods				
	November 23–December 20	December 21–January 17	January 18–February 14	February 15–March 14	March 15–April 11
1935–1936	53.5	51.3	51.4	56.2	
1933–1934	52.9	50.3	52.8	58.2	
1937–1938	55.8	49.6	50.1	52.8	51.8
1934–1935	54.1	48.8	50.9	51.6	51.9
1936–1937	51.9	44.1	44.5	53.7	51.5

NOTE: Vertical broken line marks beginning of Period II of gonad development (see p. 64); solid vertical lines mark terminations of Periods II and III.

TABLE 2

AVERAGE MAXIMUM TEMPERATURE (deg. F.)

Years	Two-week Periods									
	November 23–December 6	December 7–December 20	December 21–January 3	January 4–January 17	January 18–January 31	February 1–February 14	February 15–February 28	March 1–March 14	March 15–March 28	March 29–April 11
1935–1936........	61.9	58.8	56.6	54.9	60.5	55.6	58.0	67.8		
1933–1934........	62.4	57.4	55.4	57.1	59.6	59.9	60.1	70.1	63.1	
1937–1938........	63.0	61.2	54.2	58.3	56.6	53.1	61.0	56.4	56.4	59.9
1934–1935........	50.3	61.6	54.4	53.8	57.9	56.8	60.6	56.2	57.0	57.1
1936–1937........	58.4	59.1	51.1	47.1	47.5	53.0	57.6	65.2	55.1	59.6

Years	Three-week Periods						
	November 30–December 20	December 21–January 10	January 11–January 31	February 1–February 21	February 22–March 14	March 15–April 4	April 5–April 25
1935–1936........	59.2	56.2	58.5	56.5	64.5		
1933–1934........	57.6	57.3	57.5	60.0	66.8	64.0	
1937–1938........	61.8	55.4	57.3	53.9	59.8	56.6	
1934–1935........	61.3	54.3	56.4	58.9	56.8	57.0	
1936–1937........	58.8	49.5	47.6	54.5	62.7	56.2	62.6

Years	Four-week Periods				
	November 23–December 20	December 21–January 17	January 18–February 14	February 15–March 14	March 15–April 11
1935–1936........	60.4	55.8	58.1	62.9	
1933–1934........	59.9	56.3	59.8	65.1	
1937–1938........	62.1	56.3	54.8	58.4	58.1
1934–1935........	60.9	54.1	57.4	58.4	57.4
1936–1937........	58.7	49.1	50.3	61.4	57.4

TABLE 3
AVERAGE MINIMUM TEMPERATURE (deg. F.)

Two-week Periods

Years	November 23-December 6	December 7-December 20	December 21-January 3	January 4-January 17	January 18-January 31	February 1-February 14	February 15-February 28	March 1-March 14	March 15-March 28	March 29-April 11
1935–1936	48.6	44.7	45.6	48.0	45.7	43.8	48.1	50.6		
1933–1934	46.1	45.5	45.2	43.5	45.2	46.6	50.2	52.2	51.1	
1937–1938	49.1	49.9	41.7	43.6	45.2	45.1	46.7	47.1	45.9	44.9
1934–1935	46.9	47.7	42.8	44.2	43.0	46.1	45.6	43.7	42.6	48.9
1936–1937	44.6	45.6	42.3	36.0	35.7	41.9	42.4	49.4	44.4	46.6

Three-week Periods

Years	November 30-December 20	December 21-January 10	January 11-January 31	February 1-February 21	February 22-March 14	March 15-April 4	April 5-April 25
1935–1936	45.6	46.5	46.4	46.1	48.9		
1933–1934	44.8	45.4	43.9	48.0	51.3	51.0	
1937–1938	49.6	41.8	45.2	44.1	48.6	45.0	
1934–1935	47.1	43.9	42.8	46.2	44.2	45.2	
1936–1937	45.0	39.6	36.4	41.9	47.2	45.2	49.9

Four-week Periods

Years	November 23-December 20	December 21-January 17	January 18-February 14	February 15-March 14	March 15-April 11
1935–1936	46.7	46.8	44.8	49.4	
1933–1934	45.8	44.4	45.5	51.2	
1937–1938	49.5	42.7	45.2	46.9	45.4
1934–1935	47.3	43.5	44.5	44.8	45.7
1936–1937	45.1	39.1	38.9	45.9	45.5

TABLE 4

NUMBER OF DAYS MEAN TEMPERATURE ABOVE 50° F.

Years	Two-week Periods									
	November 23-December 6	December 7-December 20	December 21-January 3	January 4-January 17	January 18-January 31	February 1-February 14	February 15-February 28	March 1-March 14	March 15-March 28	March 29-April 11
1935–1936	9	10	8	10	11	5	11	14		
1933–1934	3	9	7	5	8	11	12	14	9	
1937–1938	14	14	3	7	8	4	8	8	8	11
1934–1935	6	11	2	3	2	7	11	6	5	12
1936–1937	3	11	0	0	0	2	6	14	5	14

	Three-week Periods						
	November 30-December 20	December 21-January 10	January 11-January 31	February 1-February 21	February 22-March 14	March 15-April 4	April 5-April 25
1935–1936	17	13	16	12	18		
1933–1934	11	12	8	16	21	21	
1937–1938	21	10	14	5	15	12	
1934–1935	16	5	2	13	11	12	
1936–1937	14	1	0	5	17	12	21

	Four-week Periods				
	November 23-December 20	December 21-January 17	January 18-February 14	February 15-March 14	March 15-April 11
1935–1936	19	18	16	25	
1933–1934	12	12	19	26	
1937–1938	28	10	12	16	19
1934–1935	17	5	9	17	17
1936–1937	14	1	2	20	19

TABLE 5

NUMBER OF DAYS MAXIMUM TEMPERATURE ABOVE 55° F.

Years	Two-week Periods									
	November 23–December 6	December 7–December 20	December 21–January 3	January 4–January 17	January 18–January 31	February 1–February 14	February 15–February 28	March 1–March 14	March 15–March 28	March 29–April 11
1935–1936	13	11	10	7	11	5	12	14		
1933–1934	12	9	8	6	9	10	14	14	11	
1937–1938	14	13	4	10	8	3	10	8	6	11
1934–1935	14	12	8	2	9	7	12	7	7	12
1936–1937	9	11	1	0	0	1	10	14	7	14

Years	Three-week Periods						
	November 30–December 20	December 21–January 10	January 11–January 31	February 1–February 21	February 22–March 14	March 15–April 4	April 5–April 25
1935–1936	17	14	14	12	19		
1933–1934	15	13	10	17	21	20	
1937–1938	20	8	14	6	15	10	
1934–1935	19	9	10	14	12	13	
1936–1937	15	1	0	7	18	14	21

Years	Four-week Periods				
	November 23–December 20	December 21–January 17	January 18–February 14	February 15–March 14	March 15–April 11
1935–1936	24	17	16	26	
1933–1934	21	14	19	28	
1937–1938	27	14	11	18	10
1934–1935	26	10	16	19	19
1936–1937	20	1	1	24	21

TABLE 6

PRECIPITATION (in inches)

Years	Two-week Periods									
	November 23-December 6	December 7-December 20	December 21-January 3	January 4-January 17	January 18-January 31	February 1-February 14	February 15-February 28	March 1-March 14	March 15-March 28	March 29-April 11
1935–1936	0.03	0.59	2.51	5.43	0.36	4.84	4.10	0		
1933–1934	0.73	2.09	3.35	0.01	0.36	0.80	3.77	0	0.04	
1937–1938	0.69	4.67	1.01	0.51	2.50	7.84	1.28	3.59	2.74	1.29
1934–1935	0.08	1.90	2.09	5.57	0.46	0.70	1.99	1.40	2.03	3.47
1936–1937	0	0.35	3.09	2.84	2.61	4.62	1.38	1.74	6.73	0.72

Years	Three-week Periods						
	November 30-December 20	December 21-January 10	January 11-January 31	February 1-February 21	February 22-March 14	March 15-April 4	April 5-April 25
1935–1936	0.62	5.11	3.19	7.89	1.05		
1933–1934	2.82	3.35	0.37	2.18	2.39	0.20	
1937–1938	4.68	1.01	3.01	8.44	4.27	4.03	
1934–1935	1.95	5.77	2.35	0.85	3.33	2.95	
1936–1937	0.35	3.74	4.80	4.80	2.94	6.79	.67

Years	Four-week Periods				
	November 23-December 20	December 21-January 17	January 18-February 14	February 15-March 14	March 15-April 11
1935–1936	0.62	7.94	5.20	4.10	
1933–1934	2.82	3.36	1.16	3.77	
1937–1938	5.36	1.62	1.56	4.87	4.03
1934–1935	1.98	7.66	1.16	3.39	5.50
1936–1937	0.35	5.93	7.23	3.12	7.45

TABLE 7

PERCENTAGE OF POSSIBLE HOURS OF SUNSHINE

Years	Two-week Periods									
	November 23-December 6	December 7-December 20	December 21-January 3	January 4-January 17	January 18-January 31	February 1-February 14	February 15-February 28	March 1-March 14	March 15-March 28	March 29-April 11
1935–1936	58.4	74.4	49.6	38.1	75.8	63.8	58.4	97.0		
1933–1934	25.4	9.4	18.1	36.9	32.9	31.7	15.6	60.1	38.5	
1937–1938	78.9	48.1	31.6	58.6	52.1	6.8	57.9	30 0	52.9	72.4
1934–1935	53.9	42.9	43.4	39.6	51.4	35.4	65.5	49.2	51.0	29.2
1936–1937	55.1	49.2	29.8	43.1	59.6	32.6	68.1	56.3	28.9	52.9

	Three-week Periods						
	November 30-December 20	December 21-January 10	January 11-January 31	February 1-February 21	February 22-March 14	March 15-April 4	April 5-April 25
1935–1936	62.9	44.3	64.7	55.2	90.9		
1933–1934	11.4	29.5	29.0	26.0	45.6	47.7	
1937–1938	59.6	48.1	46.7	22.6	45.7	56.0	
1934–1935	57.4	41.7	48.1	37.4	52.3	41.7	
1936–1937	56.2	39.7	48.6	47.4	57.3	35.9	70.7

	Four-week Periods				
	November 23-December 20	December 21-January 17	January 18-February 14	February 15-March 14	March 15-April 11
1935–1936	66.4	43.8	69.8	77.7	
1933–1934	17.4	27.5	32.2	37.9	
1937–1938	63.5	45.1	29.4	40.4	62.6
1934–1935	48.4	41.6	43.4	57.1	40.1
1936–1937	51.2	36.4	46.1	62.2	40.9

APPENDIX III

Testis Volumes of Berkeley Pugetensis Previous to Migration

(Graphed in figs. 20–24)

Date	1935 No.	1935 Volume	1935 Average Volume	1936 No.	1936 Volume	1936 Average Volume	1937 No.	1937 Volume	1937 Average Volume	1938 No.	1938 Volume	1938 Average Volume
March 1...	...	...	...	...	...	...	...	...	...	1	2.71	2.71
March 5...	...	...	...	2	2.26 *2.32	2.29	...	...	...	...	...	...
March 7...	...	...	...	5	*4.98 *2.59 1.84 2.46 2.15	2.80	...	...	...	...	...	...
March 8...	...	...	...	...	...	...	...	...	...	4	1.51 1.74 2.71 3.47	2.36
March 11...	...	...	...	...	...	...	...	...	...	1	2.79	...
March 13...	...	...	...	...	...	...	...	...	...	2	3.48 3.78	...
March 14...	...	...	...	...	...	...	5	1.96 1.57 1.93 1.43 .84	1.55	...	...	...
March 15...	...	...	...	1	*3.54	3.54	...	...	...	...	...	...
March 19...	...	...	...	4	*3.33 *4.29 1.68 2.95	3.07	...	...	...	...	...	...

APPENDIX III (Continued)

Date	1935 No.	1935 Volume	1935 Average volume	1936 No.	1936 Volume	1936 Average Volume	1937 No.	1937 Volume	1937 Average Volume	1938 No.	1938 Volume	1938 Average Volume
March 20...	4	1.83 1.77 *4.44 *5.26	3.33	...	...	...	...	...	...	7	1.59 2.82 3.08 *3.35 *3.75 *4.69 6.08	3.62
March 25...	...	...	...	...	...	...	5	1.57 *5.45 3.10 3.72 3.72	5.51	...	...	...
March 27...	2	2.32 *2.55	2.44	...	...	...	...	...	...	7	*3.10 *3.93 *9.41 2.03 1.68 *5.10 *3.03	4.04
March 28...	3	*4.78 *3.23 *3.21	3.74	...	...	...	...	...	...	...	...	...
April 3...	3	*2.36 2.16 *2.16	2.23	...	...	...	5	*5.15 *3.95 *12.42 2.70 2.35	4.29	1	*3.93	3.93
April 4...	...	...	...	...	...	...	...	...	...	1	*2.66	2.66
April 7...	1	*4.91	4.91	...	...	...	...	...	...	...	...	...

* Bird ready to migrate.

APPENDIX IV

TESTES OF BIRDS ARRIVING AT NORTHERN STATIONS

Place	Date	Number of Birds	Volume (mm.³)	Volume range (mm.³)	Average volume (mm.³)
Tillamook............	April 2, 1935	3	8.6	4.8 – 8.6	5.76
			5.4		
			4.8		
	April 5, 1935	1	11.3		
	April 7, 1935	1	8.3		
	April 12, 1935	3	4.7	4.7 – 12.6	7.93
			6.49		
			12.6		
	April 16, 1935	1	24.13		
	April 11, 1936	2	34.32	33.99–34.32	34.16
			33.99		
	April 13, 1936	1	7.38		
	April 25, 1936	2	1.32		
			41.56		
	April 10, 1937	3	19.12	19.12–35.30	22.56
			13.27		
			35.20		
Friday Harbor.......	April 7, 1936	1	48.9		
	April 9, 1936	1	30.2		
	April 10, 1936	5	69.8	33.3– 78.3	55.26
			78.3		
			34.8		
			33.3		
			60.0		
	April 11, 1936	4	57.1	38.7– 66.1	55.7
			66.1		
			38.7		
			61.1		
	April 14, 1936	2	69.7	55.4– 69.7	62.55
			55.4		
	April 16, 1936	2	45.2	40.9– 45.16	43.05
			40.9		
	April 17, 1936	2	38.0	38.0–105.9	71.95
			105.9		
	April 19, 1936	4	60.8	60.8–252.5	135.00
			252.5		
			133.9		
			92.6		
	April 20, 1936	4	62.8	57.2–196.9	108.25
			57.2		
			196.9		
			116.1		
	April 21, 1936	1	37.2		
	April 22, 1936	2	44.8	44.8–140.3	92.55
			140.3		
	April 24, 1936	1	75.2		

APPENDIX IV (*Continued*)

Place	Date	Number of Birds	Volume (mm.³)	Volume range (mm.³)	Average volume (mm.³)
	April 26, 1936	2	114.5 117.8	114.5–117.8	116.15
	May 1, 1936	2	103.4 98.6	98.6–103.4	100.50
Sea Island, B. C......	April 16, 1934	3	68 1 38.0 53.3	38.0– 68.1	53.13
Comox, B. C., and Merville, B. C......	April 15, 1936	10	79.5 76.0 120.6 158.5 28.9 88.5 93.4 51.7 103.4 74.2	28.9–158.5	87.47
	April 27, 1936	6	149.0 112.4 102.1 82.7 68.6 182.3	68.6–182.3	116.20

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EXPLANATION OF PLATES
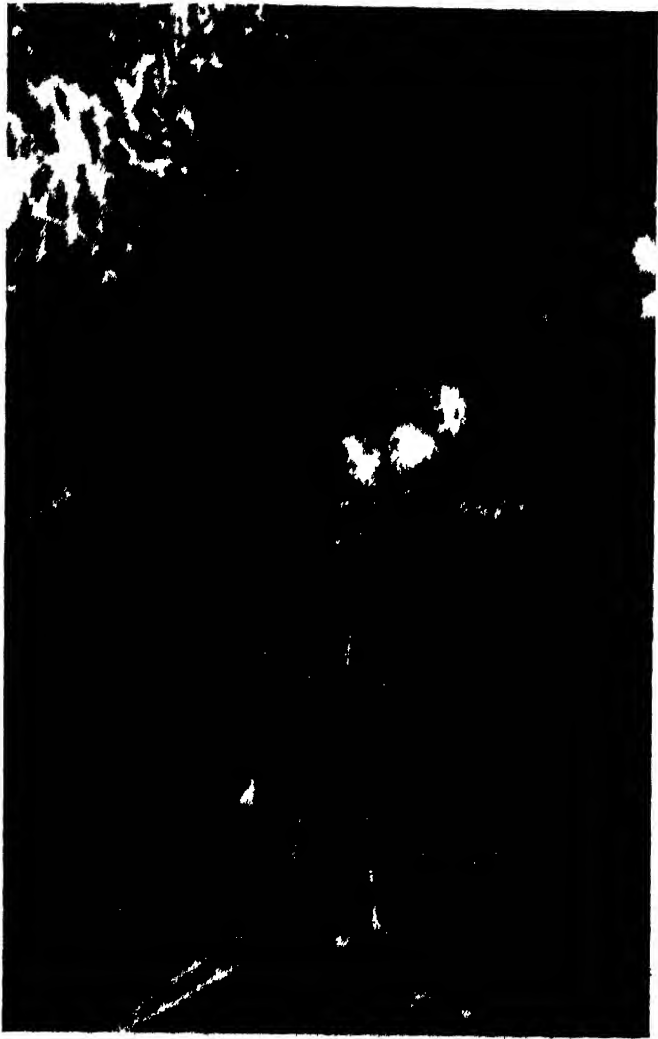
PLATE 2

Nuttall sparrow nestling four hours after hatching. Approximately life size. Photographs taken May 14, 19_5, by Mary M. Erickson.

a

b

PLATE 3

a Female Nuttall sparrow and young. Point Lobos, Monterey County, California

b Female removing fecal sac from nest

Photographs taken May 20, 1937, by Ludlow O. Williams

a
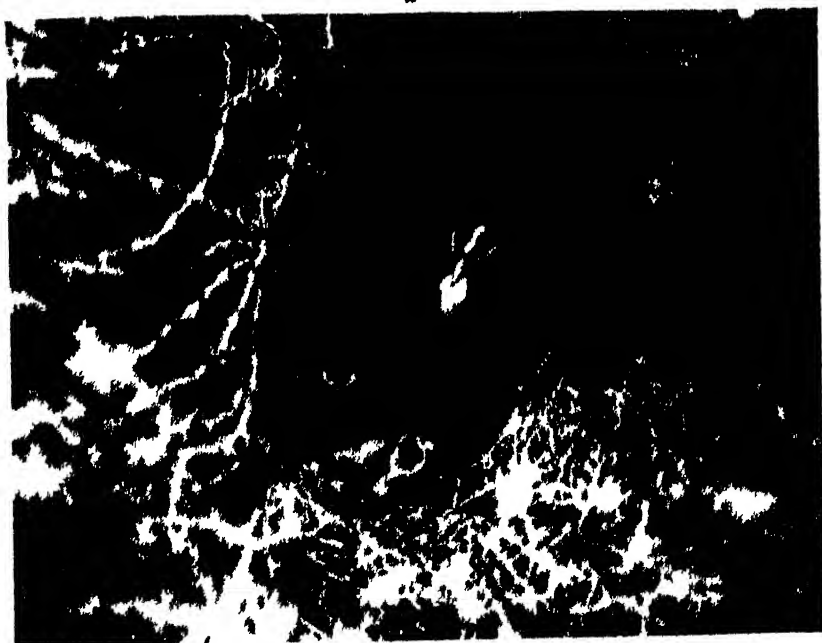
b

PLATE 1

Testes of Nuttall sparrow showing increase in size from inactive to breeding condition. Approximately × 1½. Photograph by W. C. Matthews, Berkeley, California.
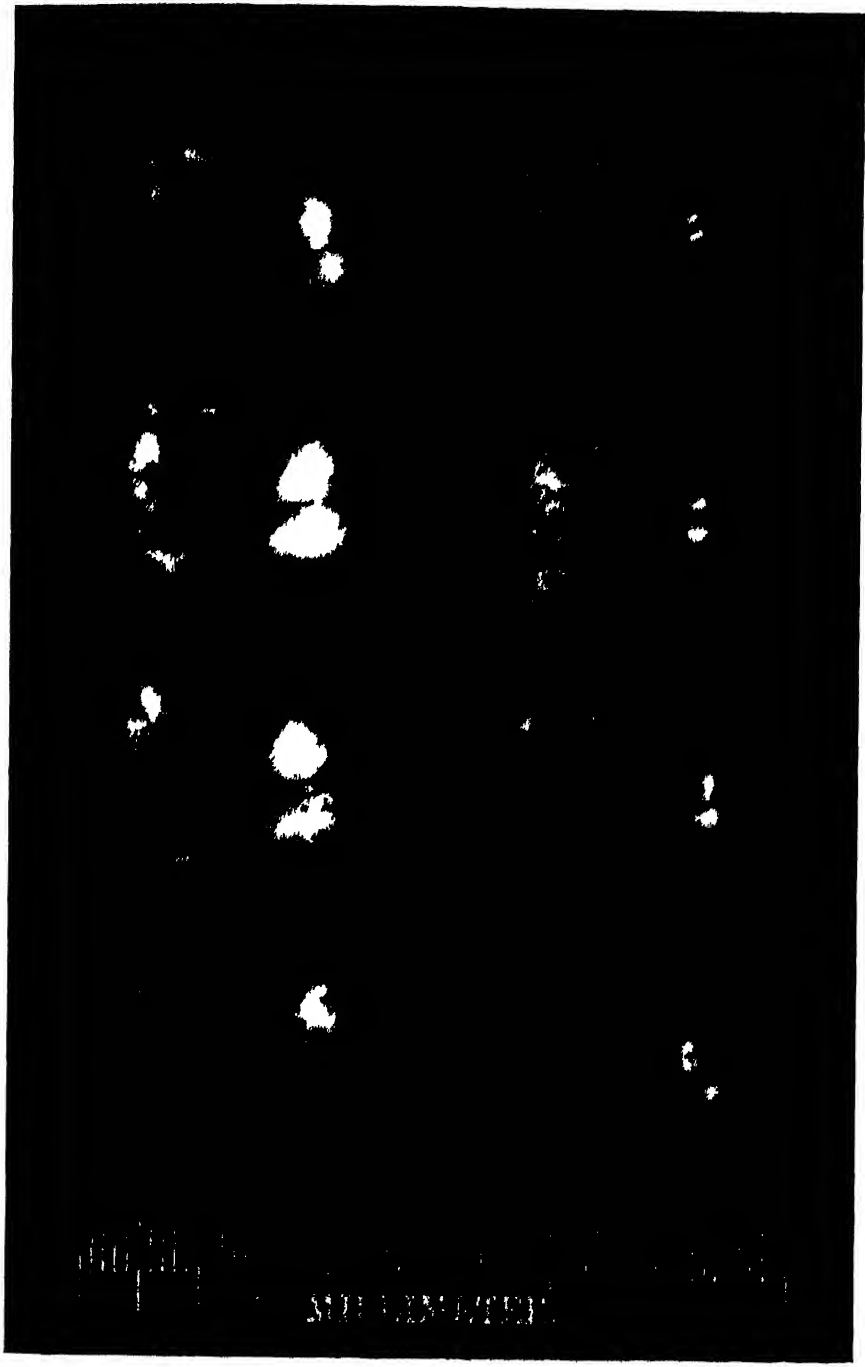
Photomicrographs of Nuttall sparrow testes

PLATE 5

Stage 1 Inactive condition. No interstitial cells

a × 50

b × 325

a

b

PLATE 6

Stage 2. First change from inactive condition. Interstitial cells appearing.

a. × 60. Tunica albuginea accidentally removed.

b. × 325.
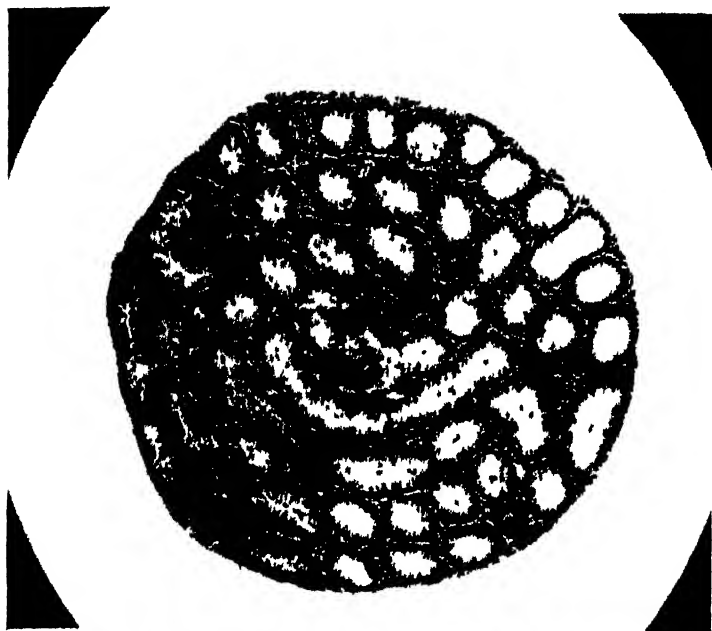
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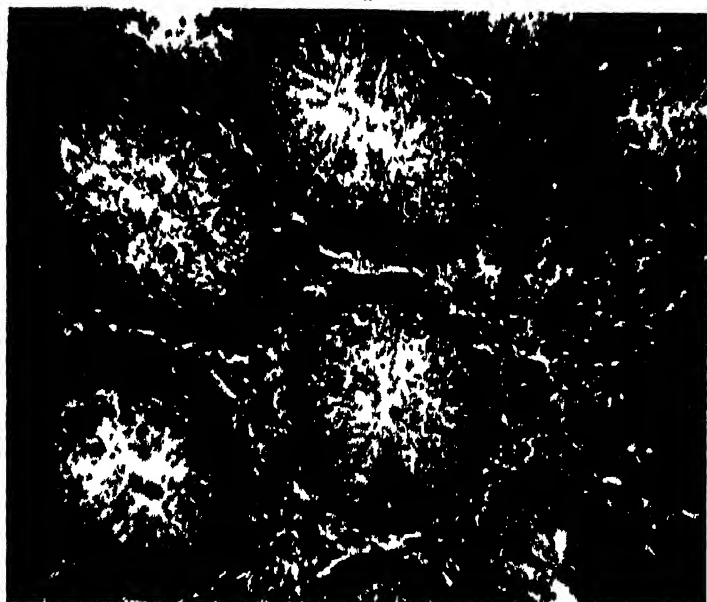
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PLATE 7

Stage 3. Marked increase in germinal elements and in-
terstitial cells.

a. × 80.
b. × 325.
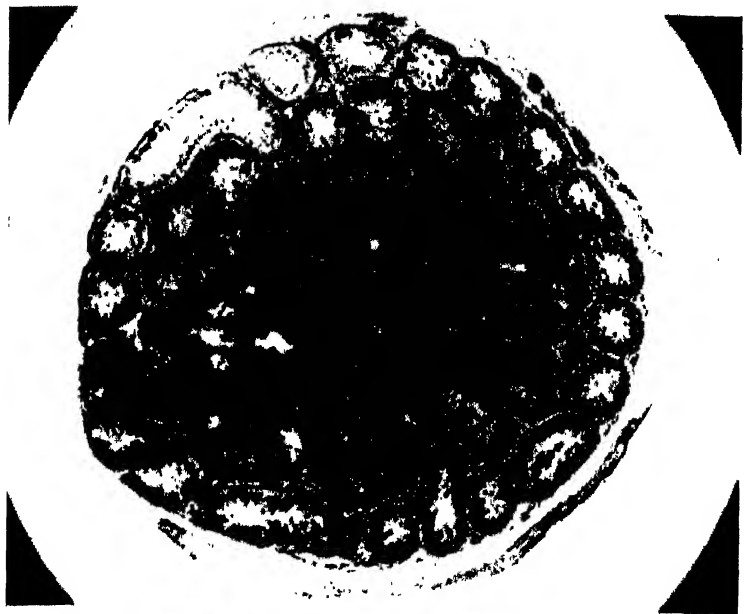
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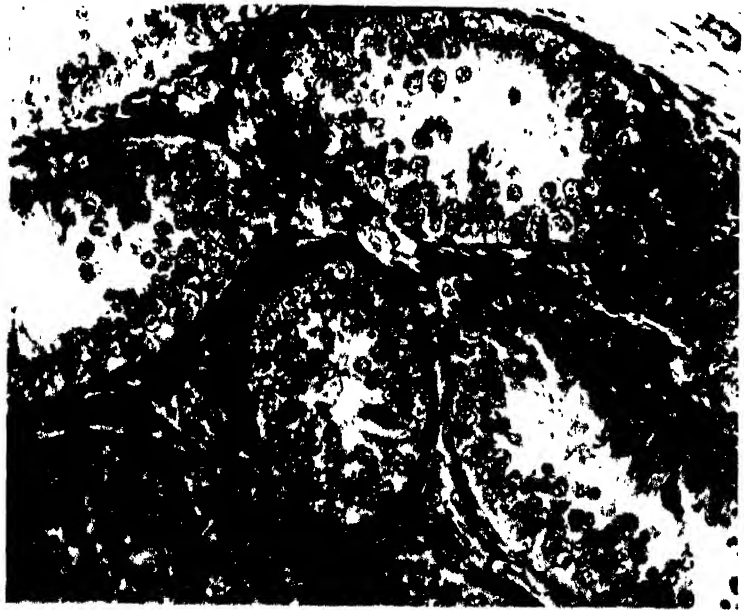
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PLATE 8

Stage 4. Primary spermatocytes in synapsis. Interstitial cells at maximum.

a. × 80.

b. × 325.
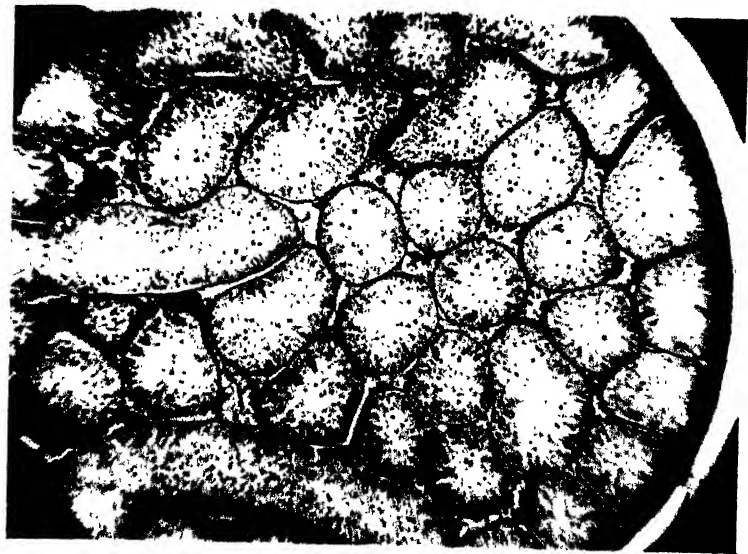
a

b

PLATE 9

Stage 4 Primary spermatocytes in synapsis Interstitial cells × 325
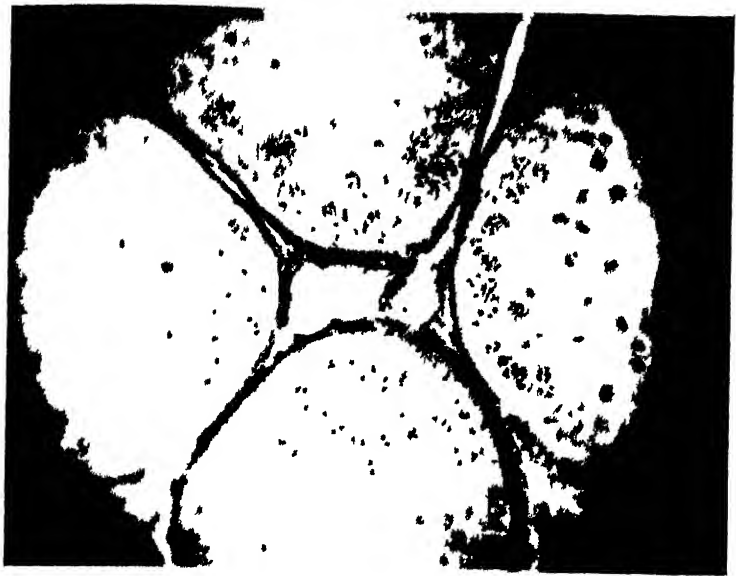
PLATE 10

Stage 5 Predominance of primary spermatocytes in
synapsis

a × 50

b × 25

a
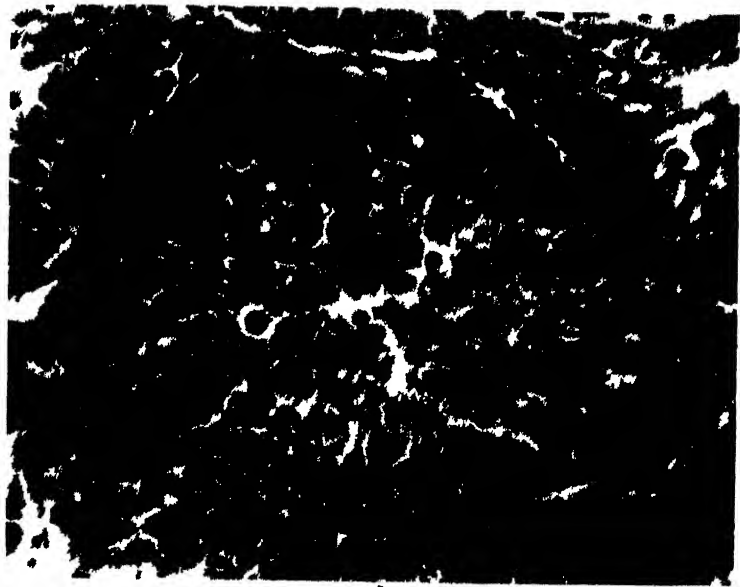
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PLATE 11

Stage 6 (early). Spermatids present.

a. × 80.
b. × 325.
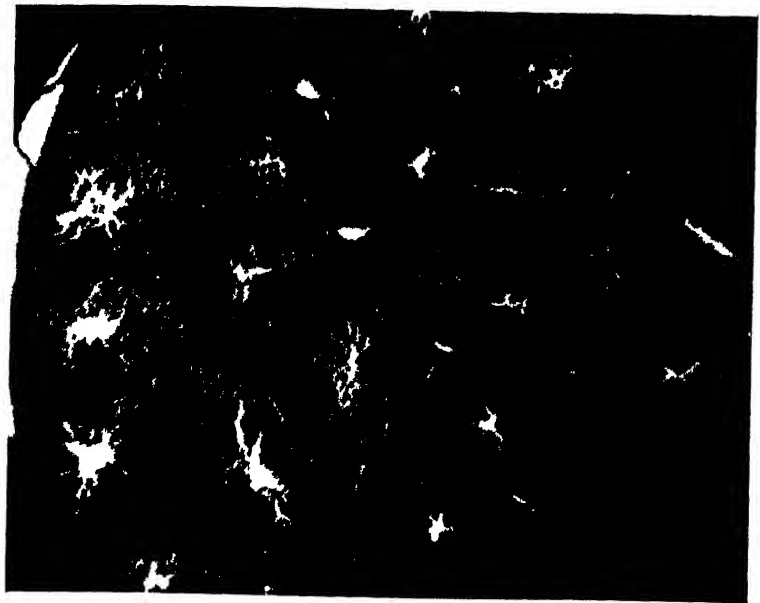
a

PLATE 12

Stage 6 (late) Spermatids in metamorphosis.

a. × 80.

b × 325.

a
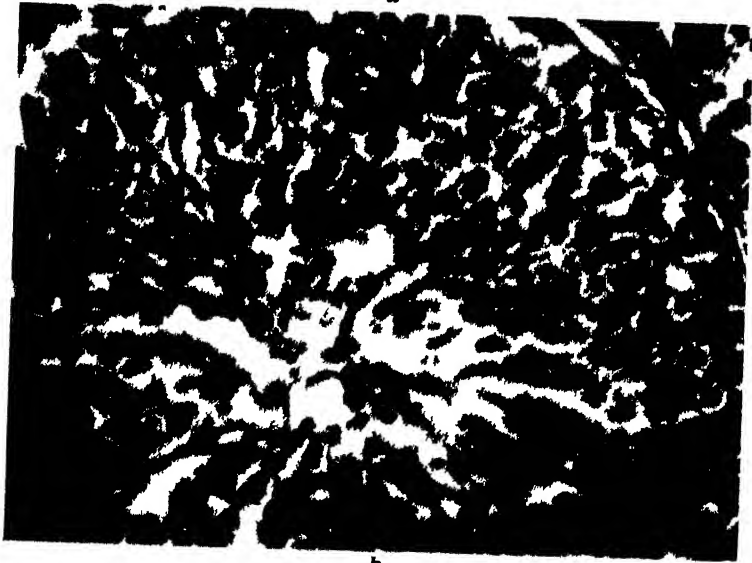
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PLATE 13

Stage 7. Breeding condition. Mature sperms grouped in bundles

a × 80 Showing thinness of tunica albuginea.

b. × 325.

a

b

PLATE 14

a × 325 Stage 7 Mature sperms free in lumen

b × 325 Stage 7 Showing blood vessels and a few interstitial cells in space between tubules

a

b

PLATE 15

Regression (only)

a ✕ 50 Showing thickness of tunica albuginea

b ✕ 25
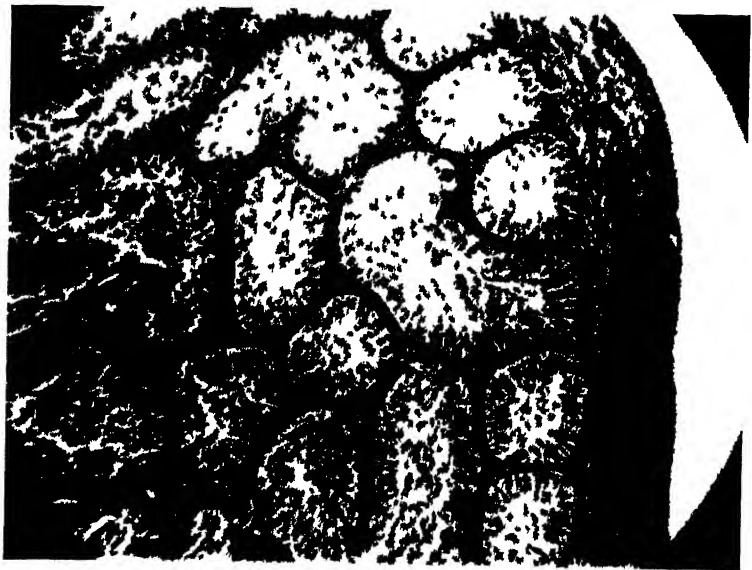
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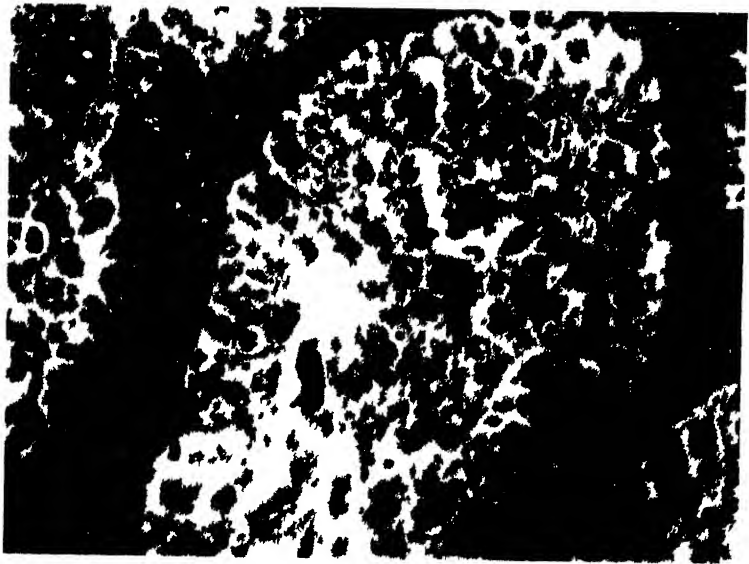
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PLATE 16

Regressive stage (late). All cells in tubules degenerating except spermatogonia. Intertubular material at maximum.

 a. × 80.
 b. × 325.
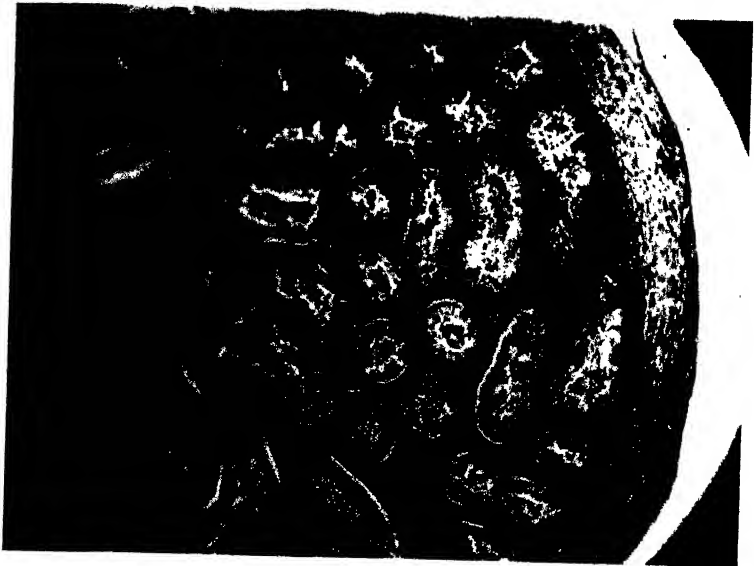
a

b

a

b

PLATE 18

Most advanced of Berkeley Puget Sound sparrows.

a. × 80.
b. × 325.
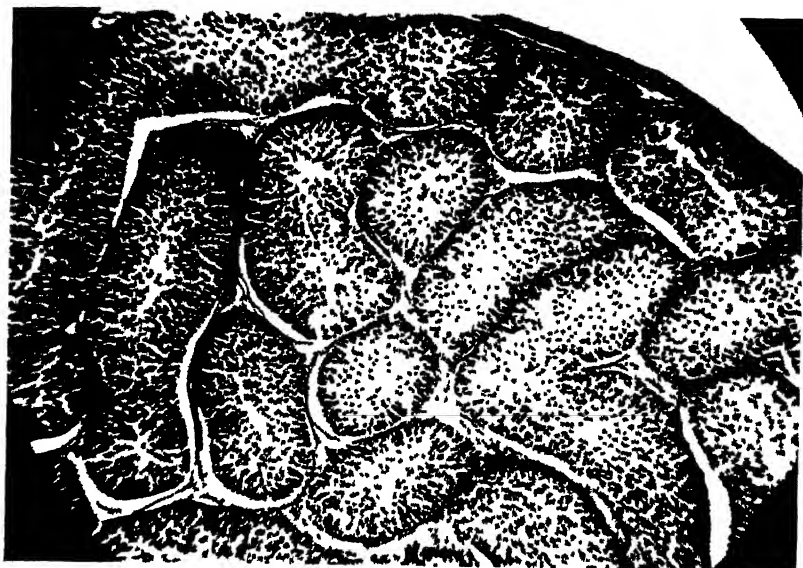
a

b

PLATE 19

Puget Sound sparrow at Victoria, B. C., prior to fall migration. Absence of functional interstitial cells.

a. × 80.
b. × 325.
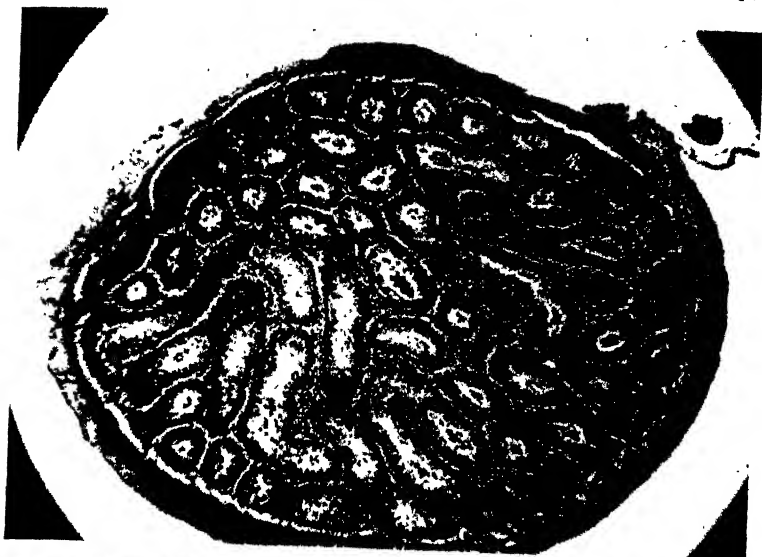
a
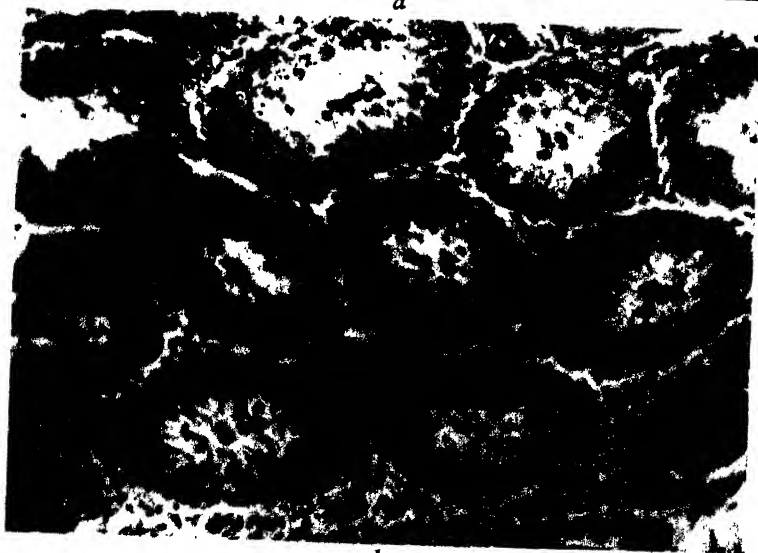
b

PLATE 20

Puget Sound sparrow, Victoria, B C Regression Reconstitution of intertubular material

   a ✕ 80
   b ✕ ?25

a

b

THE NATURAL HISTORY AND CLASSIFICATION OF THE MOUNT LYELL SALAMANDER, HYDROMANTES PLATYCEPHALUS

BY

LOWELL ADAMS

THE NATURAL HISTORY AND CLASSIFICATION OF THE MOUNT LYELL SALAMANDER, HYDROMANTES PLATYCEPHALUS

BY

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(Contribution from the Museum of Vertebrate Zoology of the University of California)

INTRODUCTION

THE MOUNT LYELL SALAMANDER was discovered and named in 1916 by Camp, who recognized its close resemblance to *Oedipus* (*Spelerpes*) of Mexico, and accordingly placed it in that genus. Later, Dunn (1923) transferred it to the genus *Hydromantes*. This genus is at present composed of only two full species, *Hydromantes genei* of Sardinia and the mainland of Italy, and *Hydromantes platycephalus* of the Sierra Nevada of California. *Hydromantes italicus* has been reduced to subspecific status under *H. genei* by Wolterstorff (1925), and Pomini (1936) was unable to verify the existence of *ferrugineus*, which Lazzarini (1930) assigned to the genus *Hydromantes*. The zoögeographic significance of the discontinuous distribution of *Hydromantes* is emphasized by Dunn: "The most startling discovery made in the United States since Stejneger announced the finding of a discoglossal toad in the Olympic Mountains was that of *Spelerpes platycephalus* in the Yosemite by Camp." Dunn's reference of *platycephalus* to the genus *Hydromantes* was based on examination of only two specimens. An understandable reluctance on Dunn's part to dissect any of the then few known specimens and thus destroy certain external characters would explain why he did not cite many features of internal structure in support of his generic identification. This omission, especially in view of the importance ascribed to the identification, led me to undertake an independent appraisal of the relationships of the Mount Lyell salamander. With more specimens available, selected parts of the internal anatomy were investigated to provide a wider basis for judging the animal's affinities.

My interest in the Mount Lyell salamander dates from 1935, when I was rearranging the study collections of the Yosemite Museum. About 25 specimens were then in the collections—probably three-fourths of all the known material. These formed the nucleus for the present study.

For many helpful suggestions and criticisms I am indebted to Professor E. Raymond Hall, under whose supervision this work has been done, and to Professor Charles L. Camp, Professor Alden H. Miller, and Dr. Jean M. Linsdale. Mr. James E. Cole aroused my initial interest in the problem, and lent specimens from the Yosemite Museum. Other specimens came from the California Academy of Sciences, Stanford University, and Wilbur V. Henry, who graciously lent me the specimens which he himself had planned to use in a similar study. I did most of the present work at the Museum of Vertebrate Zoölogy through the kindness of the late Professor Joseph Grinnell. Mr.

Thomas L. Rodgers has assisted with the staining of skeletons, and Professor E. O. Essig has kindly identified insects recovered from the stomachs of the salamanders. To these persons, and others, I wish to express my gratitude for their assistance and coöperation.

CLASSIFICATION
Genus **Hydromantes** Gistel

Hydromantes Gistel, Naturgesch. Thierr., 1848, p. XI (first use of name known to me).

Diagnosis.—Tongue boletoid; two premaxillae; a fontanelle; septomaxilla present or absent; maxilla normal; prefrontal absent; vomerine and parasphenoid series not continuous; internal nares a slit in prevomer; atlas normal; eyes functional; no aquatic larval stage; males with swollen snout and with enlarged premaxillary (sometimes also maxillary) teeth; tail not constricted at base; toes 4–5, half-webbed; terminal phalanges T-shaped; no palmar tubercles; 2 species.

Classification of the genera of plethodontids has been based largely on characters of the skull. Dunn (1926) used the following skull characters in diagnosing genera: premaxillae, fused or unfused; fontanelle, present or absent; septomaxillae, present or absent; maxillae, normal or edentulous; prefrontals, present or absent, bordering or not bordering nares; internal nares, notch or slit in prevomer; vomerine and parasphenoid teeth, continuous or discontinuous; condyles, sessile or stalked; atlas, normal or with transverse collar; other characters used by Dunn are: tongue, boletoid or attached at margin; eyes, functional or nonfunctional; sexual dimorphism, present or absent; tail constriction at base, present or absent; number of toes; amount of webbing between toes; shape of terminal phalanges; palmar tubercles, present or absent.

Piatt (1935), in an attempt to trace the ancestry of *Hydromantes*, has used characters of the hyobranchial apparatus and throat musculature. Noble (1927) and Dunn (1926) have pointed out the value of life history data in studies of phylogeny.

On the basis of the characters listed, these authors have agreed that *Hydromantes* is more closely related to *Oedipus* than to any other genus, and that both are well differentiated from other genera of plethodontids. Piatt (1935), relying on the hyobranchial apparatus and throat musculature, concluded that the *Oedipus* group developed from a *Plethodon* ancestry. Dunn (1926) assumed that *Oedipus* and *Hydromantes* arose from some terrestrial form, but made no attempt to trace their ancestry among the known terrestrial plethodontids. Noble (1931) pointed out the resemblance of the *Oedipus* group to both *Eurycea* and *Plethodon*, but reached no final conclusion regarding the immediate ancestors.

Hydromantes platycephalus (Camp)
Mount Lyell salamander

Spelerpes platycephalus Camp (1916, p. 11)
Hydromantes platycephalus, Dunn (1923, p. 40)
Eurycea platycephala, Stejneger and Barbour (1917, p. 20)

External characters (pl. 21, fig. *b*).—Adult male (Yosemite Mus., no. 171, Half Dome, 8852 feet, Mariposa County, California): 11 costal grooves; appressed toes of fore and hind feet overlap a distance of one costal fold; head width 19.6 per cent of length from tip of snout to posterior end of vent; length of head from tip of snout to gular fold, 23.9 per cent of length from tip of snout to posterior end of vent; snout not appreciably more

swollen than in females at hand; eye longer than its distance from tip of snout; mouth curved upward at the angle; angle of jaw behind posterior angle of eye; teeth on upper jaw long, irregular in size and spacing, protruding beneath upper lip, 12 on right maxilla and premaxilla; upper eyelid fitting over lower in front and behind; a groove from eye to gular fold; bulge on side of head between posterior angle of eye and angle of mouth, larger than in females at hand; limbs slightly smaller in proportion to body than those of

TABLE 1
Measurements of Total Length and Head Width (in Millimeters)

Description	Number of specimens	Range	Average length	Standard deviation
Males, length............	23	71.7–98.1	82.9 ± 1.4	6.8 ± 1.0
Females, length.........	26	71.4–97.5	79.8 ± 1.5	7.6 ± 1.0
Males, head width......	23	8.7–12.6	10.1 ± 0.2	1.0 ± 0.2
Females, head width....	26	8.2–10.8	9.6 ± 0.1	0.7 ± 0.1

TABLE 2
Measurements of Skulls (in Millimeters)

Description	*H. genei* MVZ no. 27301		*H. genei* MVZ no. 11188		*H. platycephalus* MVZ no. 32221	
	Dimensions	Per cent of skull length	Dimensions	Per cent of skull length	Dimensions	Per cent of skull length
Premaxillae to ventral lip of foramen magnum..............	11.1	100.0	12.3	100.0	9.5	100.0
Premaxillae to posterior-median tip of vomerine tooth row......	4.7	42.3	5.6	45.5	3.8	40.0
Width across frontals at narrowest point................	2.5	22.5	2.9	24.4	2.6	27.4
Width across parietals...........	3.7	33.3	4.3	35.0	3.7	39.0
Width across otic capsules.......	6.4	57.7	7.4	60.2	5.7	60.0
Depth of skull back of vomerine tooth row....................	1.6	14.4	2.1	17.1	1.4	14.7
Depth of skull anterior to otic capsules......................	2.5	22.5	2.9	23.6	1.4	14.7
Length of premaxillary spine[a].....	3.1	28.0	3.6	29.3	1.7	17.9
Length of parasphenoid tooth row	4.2 (right) 3.9 (left)		5.4 (right) 5.0 (left)		2.9 (right) 3.5 (left)	

[a] Extends to frontal in *H. genei*. Separated 0.7 mm. from frontals in *H. platycephalus*.

Triturus torosus; fingers in order of length are 3, 2, 4, 1, webbed at base; toes in order of length, 3, 4, 2, 5, 1, webbed to next to last joint; toes and fingers slightly flattened, enlarged at tips; tail circular in cross section, not constricted at base, shorter than body; cloacal lips smooth, gaping; vomerine tooth rows not continuous with tooth patches on parasphenoids, separated from each other by the width of the nares and from tooth patches of parasphenoids by 8 times that distance; teeth of parasphenoids in two distinct patches, broadest and farthest from each other near the posterior end. Color, of specimens preserved in 65 per cent alcohol: middle of back, top of head, tail and legs obscurely mottled with dark gray and dark brown, becoming lighter brown on ventral surfaces; no lichenlike markings; these are present, however, in other specimens at hand.

Variations.—Adult female (Yosemite Mus., no. 159, Half Dome): Appressed toes fail to meet by one-half costal fold; head width 18.8 per cent of length from tip of snout to posterior tip of vent; head length 23.1 per cent of length from tip of snout to posterior tip
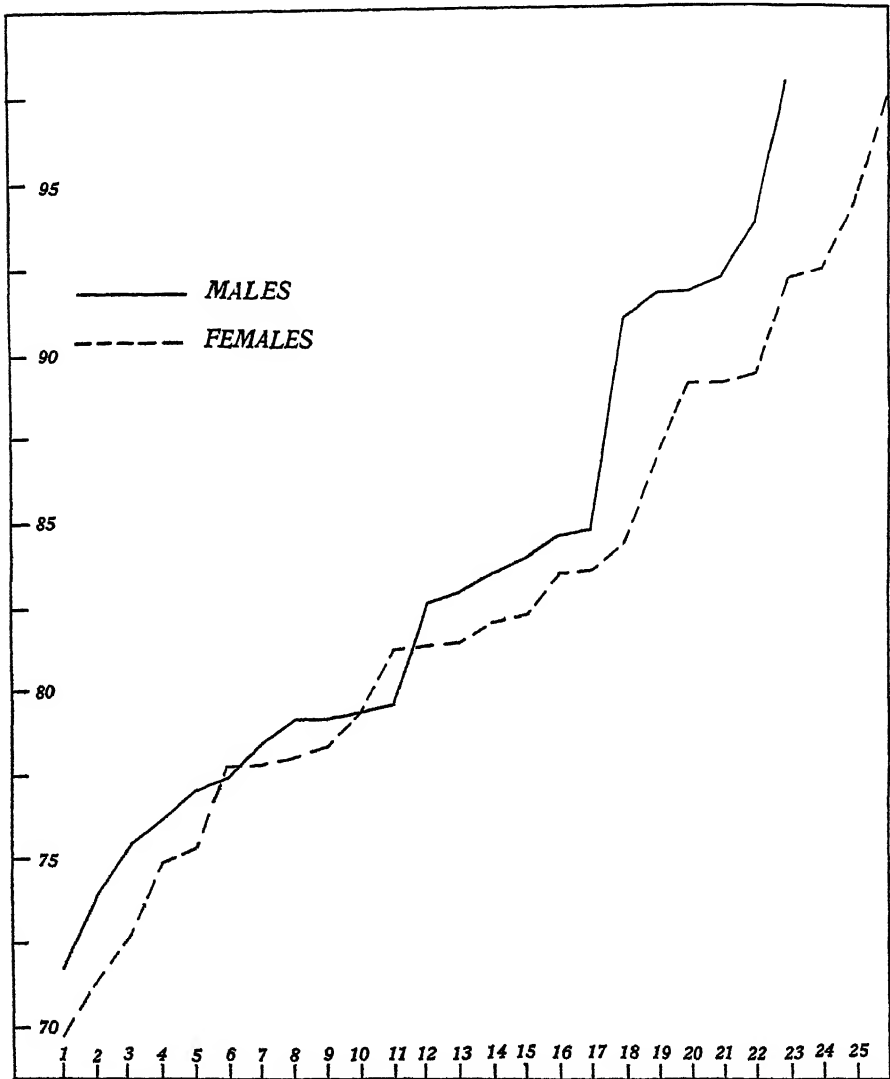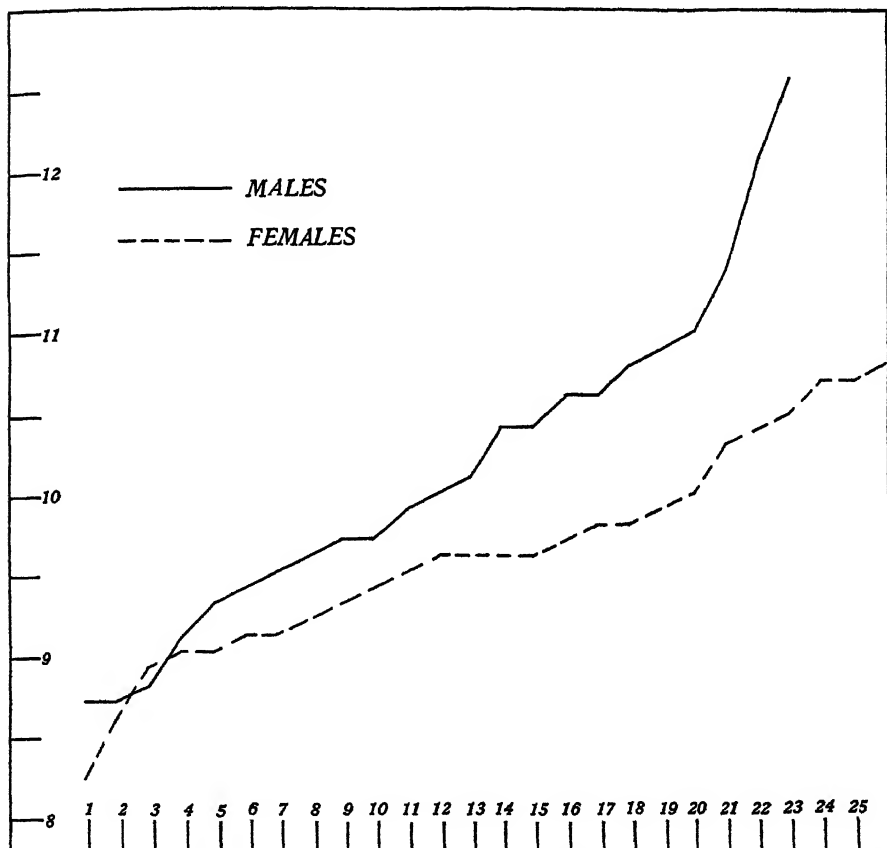

Fig. 1. Differences in total length between males and females of the Mount Lyell salamander. Numbers on ordinate indicate total length in millimeters. Salamanders numbered (shown on abscissa) in an ascending series based on size.

of vent; mouth not curved upward at the angle; teeth on upper jaw not long as in males; bulge on side of head between posterior angle of eye and angle of mouth, smaller than in males at hand; cloacal lips not gaping.

Yearling (Yosemite Mus., no. 166, Half Dome): the appressed toes overlap for a distance of one-half costal fold; head width 18.5 per cent of length of body from tip of snout to posterior tip of vent; head length 24.4 per cent of length of body from tip of snout to posterior tip of vent; head not as flat in proportion to its width as in adults; mouth not

curved upward at angle; teeth on upper jaw not long as in males; tail slightly compressed laterally along distal half; cloacal lips not gaping; color, darker brown on under parts than in adults.

Young-of-the-year (Yosemite Mus., no. 178, Half Dome): Appressed toes meet; width of head 20.5 per cent of length of body from tip of snout to posterior tip of vent; length of head 25.6 per cent of length of body from tip of snout to posterior tip of vent; snout less swollen than in intermediate sizes and adults; nostrils larger than in intermediates and

Fig. 2. Differences in head width between males and females of the Mount Lyell salamander. Numbers on ordinate indicate head widths in millimeters. Salamanders numbered (shown on abscissa) in an ascending series based on size.

adults; mouth not curved upward at the angle; teeth on upper jaw not enlarged as in adult males; no bulge at sides of head; neck as wide as head; head not as flat in proportion to its width as in adults; toes in order of length, 4, 3, 2, 5, 1; tail slightly constricted laterally in distal half; cloacal lips not gaping; brown of underparts darker than in adults.

Secondary sexual differences.—Enlarged maxillary and premaxillary teeth present in male only, and can be easily detected by rubbing fingertips across the mouth. The gaping cloaca in the male contrasts with the closed lips of the cloaca of females in all the preserved specimens examined.

In general appearance (size, color, proportions) the sexes are indistinguishable when individual specimens are considered. Nevertheless, the accompanying graphs (see figs. 1, 2) and table 1 indicate that the males average slightly larger than the females, and the difference is disproportionately greater in the group of larger animals. Blanchard (1928)
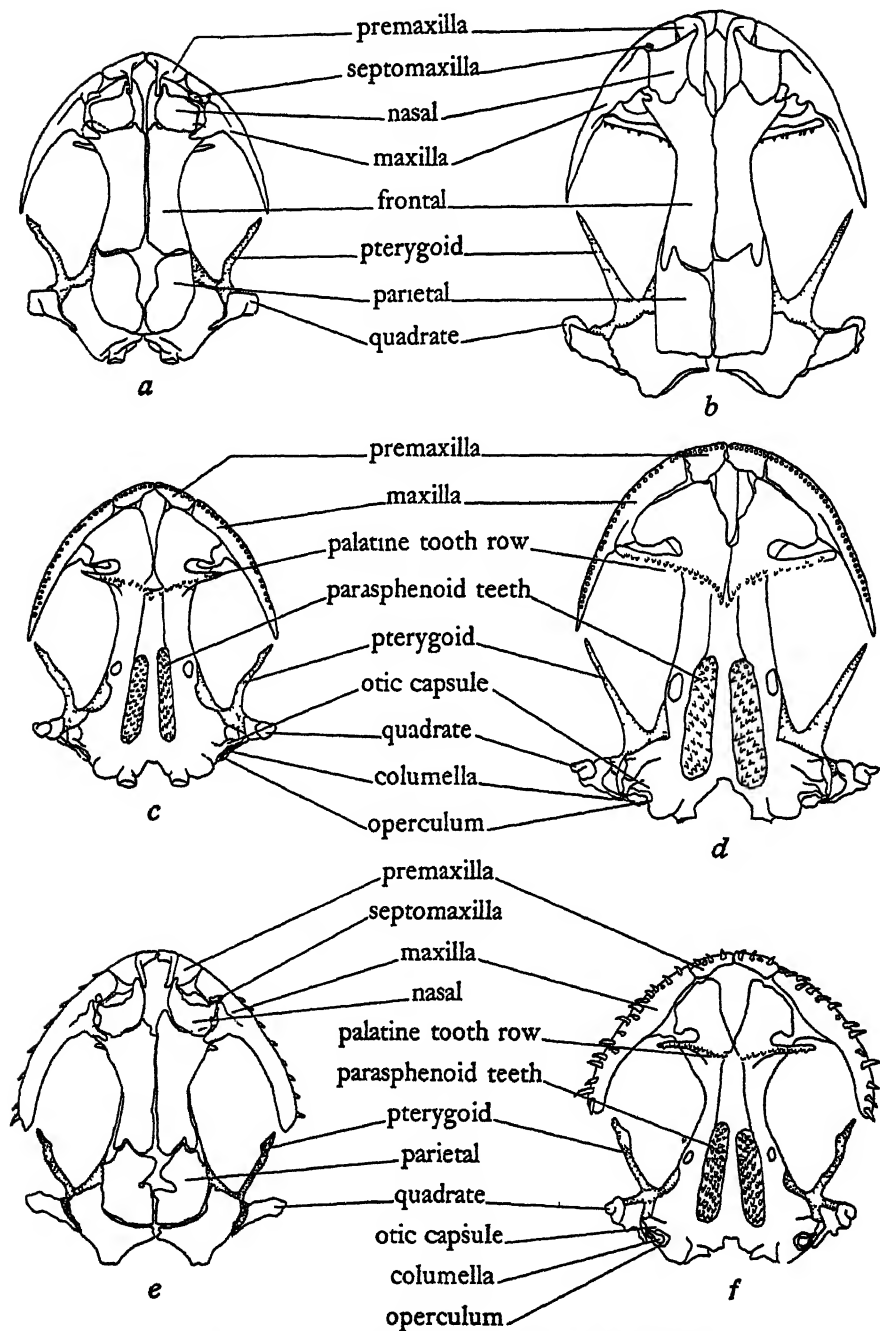
Fig. 3. Dorsal views of crania of females: (*a*) *Hydromantes platycephalus* and (*b*) *H. genei*; (*c*), (*d*) ventral views of same; (*e*) dorsal and (*f*) ventral views of male *H. platycephalus*; × 3.5.

found that in *Plethodon cinereus cinereus* the difference is just the reverse, the females being larger than the males. The difference seems slightly greater in *Plethodon*.

Skulls.—Measurements of the skulls of *Hydromantes genei* and *H. platycephalus* are given in table 2 (see also figure 3). For purposes of these comparisons skulls of two *Hydromantes genei genei* and two *H. platycephalus* were stained with alizerine red. Measurements were made with calipers calibrated to 0.1 millimeter on a vernier scale.

As shown by these measurements, the skull of an adult female of *Hydromantes platycephalus*, compared to that of *H. genei*, is shorter and more nearly flat; the brain case, relative to length of skull, is wider anteriorly and of about equal width posteriorly; ossification of
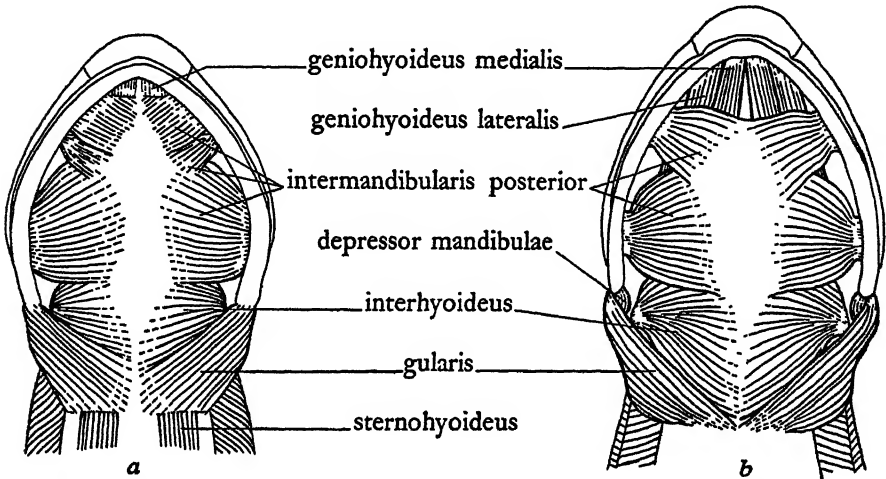
Fig. 4. Ventral view of head, with skin removed to show transverse muscles of throat and floor of mouth; (*a*) *H. platycephalus* and (*b*) *H. genei*, × 3.5.

the skull is less extensive and premaxillary spines are shorter and weaker; the vomerine tooth row, which extends laterally to the maxillae in *genei*, is considerably shorter in *platycephalus*. Other differences in size and proportion are apparent but in generic characters mentioned on page 180 the two species are alike, and the descriptions given by Dunn, Piatt, and Noble (*op. cit.*) are fully applicable to the specimens which I examined.

MUSCLES OF HEAD REGION

Further evidence of the close resemblance of *H. platycephalus* and *H. genei* is apparent upon examination of the muscles of the head region. The following descriptions and illustrations (figs. 4–7, incl.) are based on my own dissection of the muscles in four specimens of *platycephalus* and one of *genei*. Each muscle is described for *platycephalus*, and any marked differences in origins and insertions which distinguish the muscles in *genei* from those in *platycephalus* are noted.

Wiedersheim (1875) has described the musculature of the European *Hydromantes*. Piatt (1935) used the characters of the muscles of the throat in tracing the phylogeny of the Plethodontidae. Other authors (Humphrey, 1872; Druner, 1901; Lubosch, 1914; Smith, 1920; Eaton, 1936) have described and traced the phylogeny and ontogeny of the muscles of the head in various forms of salamanders. The names of muscles here employed are those used by Smith (1920) and Eaton (1936).

TRANSVERSE MUSCLES OF FLOOR OF MOUTH

M. intermandibularis posterior (Druner, 1901; Eaton, 1936) (figs. 4, 5, 6).—Thin layer of paired muscles covering most of the area between mandibles; origin along dorsal inner edge of mandibles; insertion on median fascia; divided into anterior and posterior slips
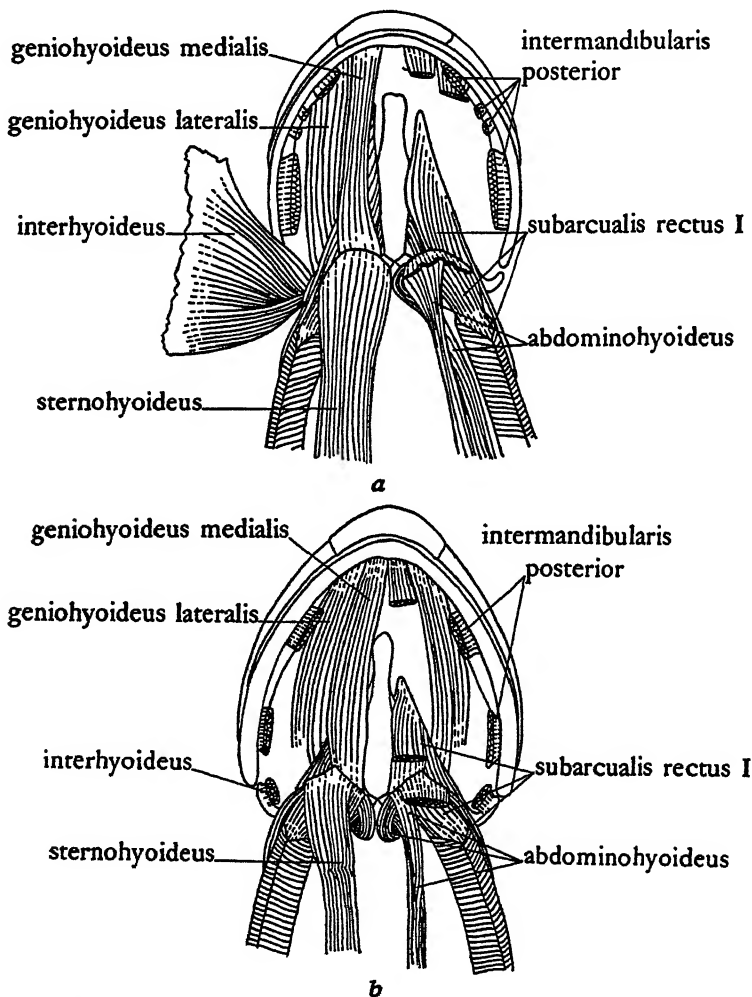
Fig. 5. Ventral view of head, with skin and superficial muscles removed to show underlying longitudinal muscles of throat and floor of mouth; (a) *H. platycephalus* and (b) *H. genei*, × 3.6.

with two small slips (or sometimes one) between. *H. genei:* small slips absent; anterior border of intermandibularis posterior more posterior than in *H. platycephalus*.

M. interhyoideus (Druner, 1901, and Eaton, 1936) (figs. 4 and 5).—Origin on lateral surface of ceratohyal along curvature near attachment of ceratohyal to quadrate; insertion broad, on median fascia; anterior third dorsal to intermandibularis posterior. *H. genei:* origin on ceratohyal near attachment to quadrate, not extending to curvature of ceratohyal.

M. gularis (Smith, 1920) (figs. 4 and 7).—The origin is on tip of mandible, on quadrate and along horizontal fold of skin posterior to eye; skin insertion marked externally by

horizontal postocular fold; insertion, anterior half on median fascia, posterior half on gular fold of skin. *H. genei:* Origin of dorsal portion not on skin but on fascia, which in turn attaches to quadrate and otic capsule (fig. 7); insertion on gular fold only.

LONGITUDINAL MUSCLES OF THE FLOOR OF THE MOUTH

M. subarcualis rectus I (Edgeworth, 1920; Eaton, 1936) (figs. 5, 6, 7).—Origin on anterior and lateral margins of ceratohyal; insertion double, medially on tendinous sheath enclos-
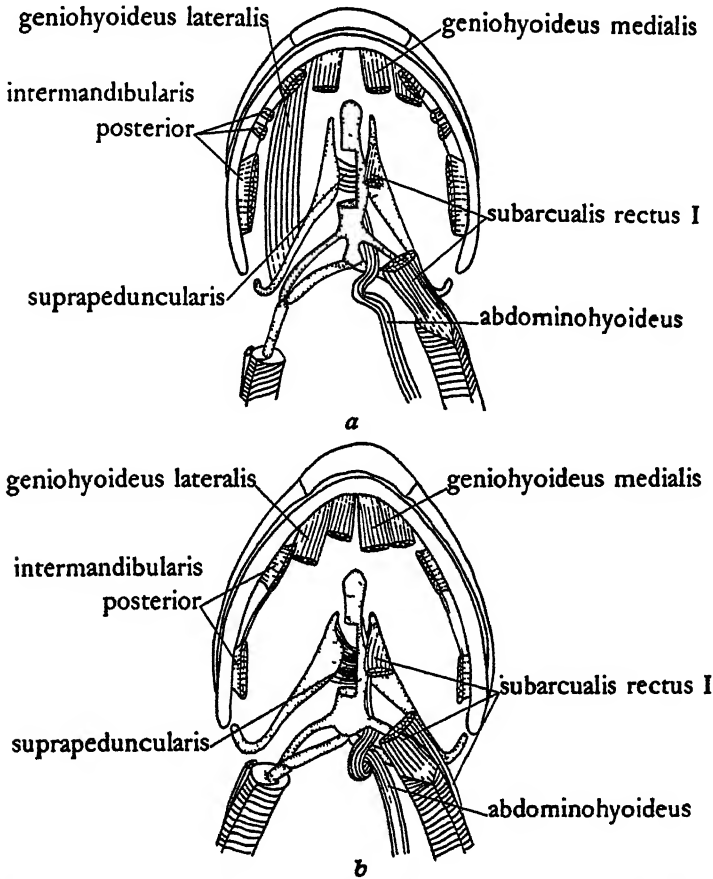
Fig. 6. Ventral view of head, showing origins and attachments of muscles of throat and floor of mouth; (*a*) *H. platycephalus* and (*b*) *H. genei,* × 3.6.

ing first epibranchial; laterally, fibers intermingle with fibers of muscular sheath of first epibranchial. *H. genei:* same.

This muscle contracts to eject the tongue. Smith (1920) suggests that it spirals around the first epibranchial in *Eurycea* to form a closed bulb which, when contracted, squeezes the epibranchial cartilage out. Apparently this mechanism is more specialized in *Hydromantes* than in *Eurycea* and, although I do not yet understand in detail how the muscle operates, I think Smith's hypothesis explains inadequately the functioning of the subarcualis rectus I in *Hydromantes*.

M. geniohyoideus lateralis (Smith, 1920) (figs. 4, 5, 6).—Origin on posterior margin of mandible lateral to origin of geniohyoideus medialis; insertion midway between ends of ceratohyal on its lateral margin. *H. genei:* lateral half of geniohyoideus lateralis inserts on membrane of mouth anterior to ceratohyal.

M. geniohyoideus medialis (Smith, 1920) (figs. 4, 5, 6).—Origin on posterior margin of mandible lateral to symphysis; insertion on the inscriptio tendinae, a connective tissue vestige of the os thyroideum. *H. genei:* same.

The os thyroideum has been lost in *Hydromantes.* Its place and function as an organ for muscular attachments has been taken by a paired mass of connective tissue, the inscriptio
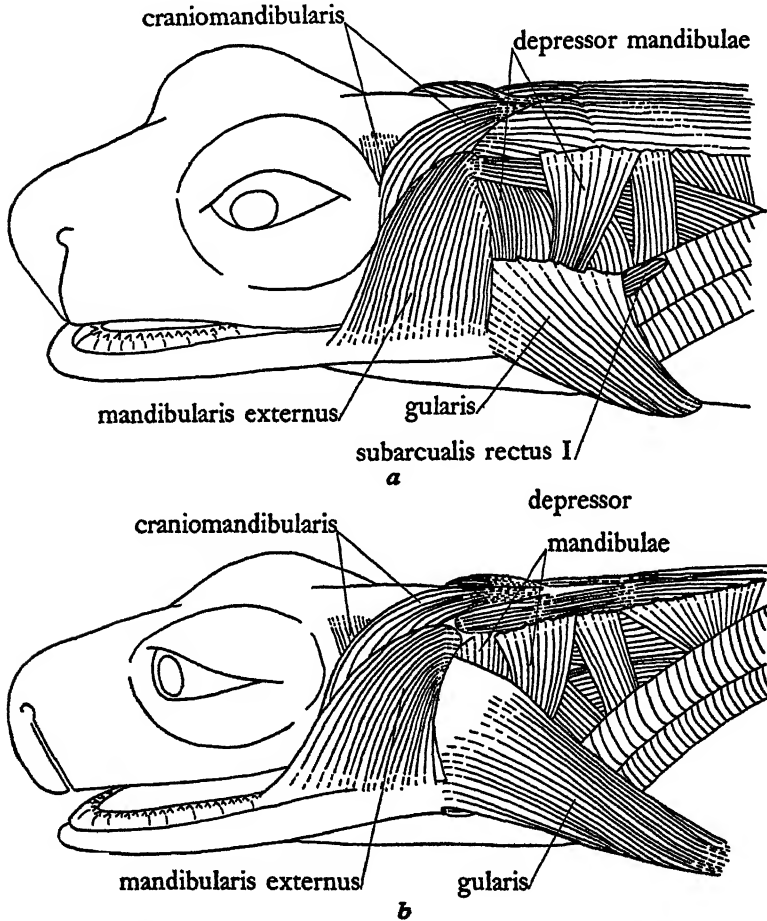
Fig. 7. Side view of head, showing jaw muscles; (*a*) *H. platycephalus* (× 2.8) and (*b*) *H. genei* (× 2.6).

tendinae (Weidersheim, 1875). These structures lie obliquely across, and attached to, the belly of the subarcualis rectus I at about its middle. The muscles that attach to the os thyroideum in other salamanders attach to the ligamentous vestiges in *Hydromantes.* The position of these vestiges in relation to other organs is different from the position of the os thyroideum illustrated by Smith (1920) in *Eurycea,* in which the bone lies directly medial to the posterior tip of the second ceratobranchial when the tongue is withdrawn into the mouth. In *Hydromantes* the inscriptio tendinae lie directly medial to the anterior tip of the second ceratobranchial.

M. sternohyoideus (Smith, 1920) (figs. 4, 5).—Anterior continuation of musculature of ventral wall of body; insertion on inscriptio tendinae and on ventral side of belly of subarcualis rectus I. *H. genei:* same.

In *Eurycea* (Smith, 1920) this muscle does not originate on the sternum. Apparently in *platycephalus* the muscle is a forward growth of the abdominal musculature of the body wall, as shown by the myocommata, which are serially arranged through the length of the abdominal musculature and continued forward in the sternohyoideus.

M. abdominohyoideus (Smith, 1920) (figs. 5, 6).—Origin on pelvic girdle; extends along body wall and into neck region parallel and dorsal to sternohyoideus, passing ventral to ceratobranchial 2, dorsal to ceratobranchial 1; inserts near tip of basibranchial; slip branching from level of pectoral girdle inserts on inscriptio tendinae dorsal and medial to insertion of sternohyoideus, opposite insertion of median half of geniohyoideus medialis. *H. genei:* same.

In contrast to the condition described in *Eurycea* by Smith (1920), the abdominohyoideus is not crossed by myocommata in *Hydromantes*.

MUSCLES OF THE JAW

M. craniomandibularis (Lubosch, 1914, and Eaton, 1936) (fig. 7).—Two parts, sublimus anterior and sublimus posterior; origin of sublimus anterior, anterolateral part of parietal bone behind supraorbital crest; insertion on membrane of mouth at base of pterygoid cartilage; origin of sublimus posterior, crest of first cervical vertebra; insertion on mandible by fusion with tendon of mandibularis externus. *H. genei:* same.

The sublimus profundus is not present in *Hydromantes*, nor are the sublimus anterior and sublimus posterior as intimately associated as in *Dicamptodon* (Eaton, 1936). Neither muscle has the origin or insertion in common with the other muscle, and the muscles do not lie parallel.

M. mandibularis externus (Lubosch, 1914, and Eaton, 1936) (fig. 7).—Origin on dorsolateral face of quadrate and on otic capsule; insertion on dorsal surface of mandible from posterior tip to angle of mouth. *H. genei:* same.

M. depressor mandibulae (Humphrey, 1872, and Eaton, 1936) (fig. 7).—Origin on lateral face of quadrate; origin of posterior slip on skin of neck and aponeurosis of dorsal muscles of neck; insertion on posterior tip of mandible. *H. genei:* No origin on aponeurosis of dorsal muscles of neck.

As indicated by the foregoing descriptions of the muscles of the head region, there is a marked similarity in these parts between *H. platycephalus* and *H. genei*. The variations in the insertion, origin, shape, and position of the muscles in the two species, and the differences noted in other structural features, indicate full specific rank for the two forms, and at the same time seem to show that the two are congeneric. These findings agree with Dunn's (*op. cit.*) conclusion that *platycephalus* and *genei* are distinct species of the genus *Hydromantes*.

NATURAL HISTORY

Distribution (see map, fig. 8).—The seven localities from which Mount Lyell salamanders are known are in the Sierra Nevada of California: near Mount Lyell, at 10,800 feet, Yosemite National Park, Tuolumne County, 8 specimens (Camp, 1916; Slevin, 1928). Silliman Gap, 10,000 feet, Sequoia National Park, Tulare County, 1 specimen (Adams, 1938). Sonora Pass, approximately 9500 feet, Alpine County, 8 specimens (Myers, 1938). Peeler Lake, 9500 feet, Mono County, at least 2 specimens (Adams, 1938). Half Dome, 8852 feet, Yosemite National Park, 100–200 specimens (Adams, 1938; Myers, 1938). Tenaya Canyon, 5800 feet, Yosemite National Park, 1 specimen (Adams, 1938). Upper Yosemite Fall, 5140 feet, Yosemite National Park, 1 specimen (Adams, 1938).

Habitat.—The geologic history of the region where the salamanders occur has been described by Matthes (1930). The rugged topography of the habitat
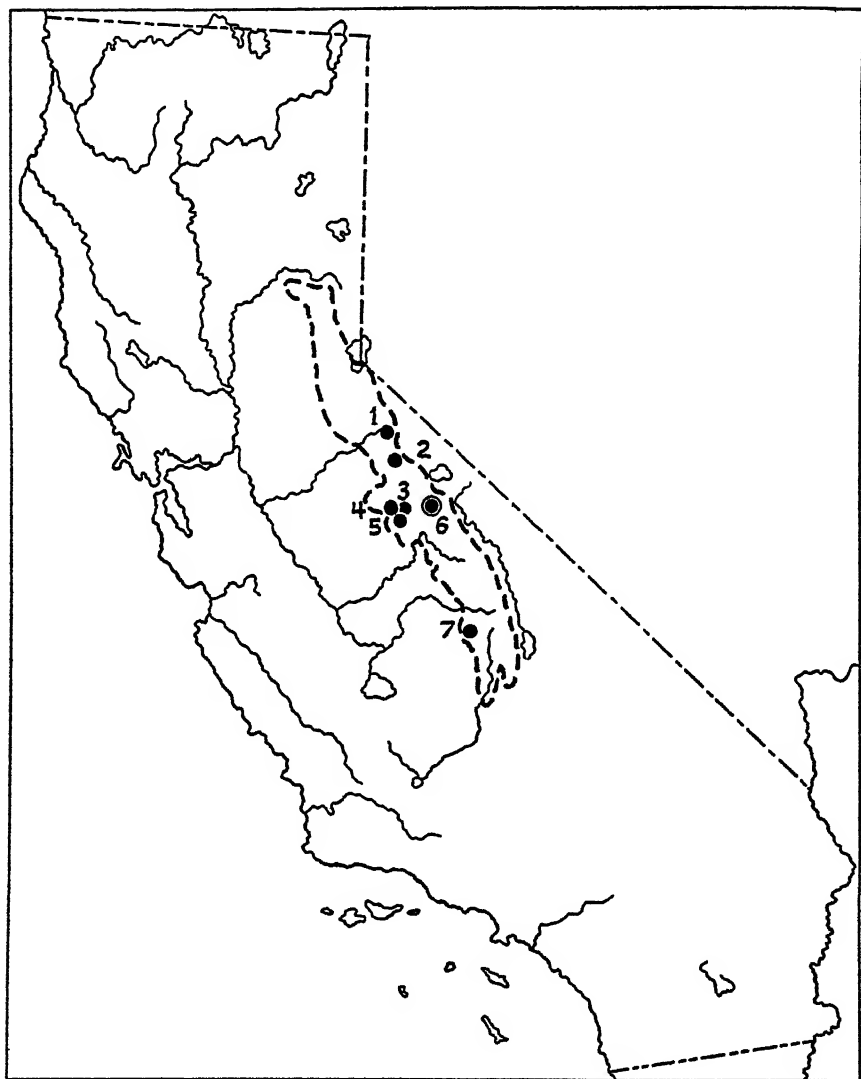
Fig. 8. Localities where Mount Lyell salamanders have been collected: (1) Sonora Pass, (2) Peeler Lake, (3) Tenaya Canyon, (4) upper Yosemite Fall, (5) Half Dome, (6) Mount Lyell, type locality, (7) Silliman Gap. The hypothetical range—the Boreal Zone in the Sierra Nevada—is outlined.

of the Mount Lyell salamander and the reclusive habits of the animal account for the comparatively recent discovery of this species and the paucity of preserved specimens.

The soil at the localities where the salamanders have been collected is remarkably similar. In the two localities with which I am personally acquainted, Half Dome and Yosemite Falls, the soil is almost entirely decomposed granite with little humus. Half Dome (pl. 21, figs. *a, b*) is topped with a veneer of flat exfoliation shells of granite under which salamanders retire in the day. What

little humus exists is furnished by a sparse vegetation composed of lichens, grasses, *Caryx* sp., *Eriogonum lobbii*, *E. marifolium*, *E. ovalifolium*, *E. wrightii*, *E. nudum*, *Sedum yosemitense*, *Stellariopsis santolinides*, *Gilia pungens*, *Pentstemon menziesii*, *Achillaea millefolium* var. *lanulosa*, and *Hieracium horridum* (Presnall, 1932). Only six scrubby trees grow on the entire 13-acre expanse of the dome's top—four lodgepole pines (*Pinus contorta murrayana*), one Jeffrey pine (*P. Jeffreyi*), and one white-bark pine (*P. albicaulis*).

In Tenaya Canyon there is much more plant growth, but even so the soil is largely mineral. Moss, lichens, and dwarfed azalea were present where a specimen was taken in Tenaya Canyon. The first two grow on the surface of granite boulders, but azalea usually grows along wooded stream banks. The type locality, north of Mount Lyell, is in terrain characterized by outcrops of granite, with occasional deposits of decomposed granite along the streams and lakes. These deposits usually support a variety of vegetation including grasses, alpine willow, heather, and scrubby white-bark pine. Camp, in his field notes dated July 18, 1915, describes the type locality as "... a large rock outcropping in a patch of heather (100 ft. in dia.) on a steep hillside (east-facing slope) above the Donohue Pass trail at 10,800 ft.... Although this heather patch lies directly in the sun almost all day, there is still snow about it and it is practically surrounded by rockslides on a bare rocky slope."

Myers's (1938) report of the Sonora Pass locality indicates edaphic conditions similar to that at Mount Lyell. He does not mention humus-producing plants.

Until the summer of 1938 all Mount Lyell salamanders had been taken at high altitudes which, according to the life-zone map of this region (Grinnell and Storer, 1924), were above the lower border of the Hudsonian. Accordingly, this salamander was thought to have been restricted to places high in the Boreal life zone. On June 18, 1938, Robert Wiegel of the Yosemite Junior Nature School found an immature salamander in Tenaya Canyon at the base of Clouds Rest. Near this locality western yellow pines, Douglas firs, and other indicators of the Transition life zone are plentiful. The salamander was found near a large deposit of avalanche snow, which remains until late in the summer, and may bring about conditions that are nearly Canadian in nature. Only a mile downstream is an island of Upper Sonoran zone which is possibly due to south exposure and reflection from the bare granite walls.

A second low-altitude find was made by me on July 29, 1938, at the base of Upper Yosemite Fall, 5140 feet. This is well within the upper border of the Transition zone. Each winter a large ice cone accumulates at the base of the fall, and this area is drenched with spray until late summer, the region thus being kept moist and cool. So many unique climatic factors exist in the immediate vicinity of the fall that they may produce there a tiny island of Canadian zone.

Thus, the Mount Lyell salamanders have been recorded from the upper border of the Transition zone upward to the upper border of the Hudsonian. The absence of records from the Arctic-Alpine zone may result from lack of

intensive effort to collect there. Far more specimens have been taken from the top of Half Dome than from all other localities combined, but this, far from being evidence that the animal is most abundant here, is a measure of the easy accessibility of the place and popular knowledge of the station. However, the dearth of recorded occurrences in the Transition life zone indicates absence of the salamanders from such low altitudes. Chance occurrences at low elevations in Yosemite may result from some salamanders falling or crawling off the edges of precipitous places and thus becoming "distributed" to lower stations, such as in Tenaya Canyon and at Yosemite Falls.

Within this salamander's range the climate (Martin, 1930) is characterized by well-defined wet and relatively dry seasons. The wet season is in winter and most of the precipitation is in the form of snow, which is most abundant from 7000–8000 feet. By July all the snow melts away at most localities below 8000 feet. On the highest peaks some snow usually remains all summer. A negligible amount of precipitation occurs as rain in the summer months.

Moisture conditions are strikingly similar at the several places where *H. platycephalus* has been found. The type locality is near a stream issuing directly from a snowfield. The stone under which 7 salamanders were found at Sonora Pass was wet by the splash of a small stream from a snowbank. A snowbank was reported near the station of occurrence at Silliman Gap. Although no spray was produced there, the salamander was found in the late evening when the relative humidity was presumably higher than in the daytime. Barren rocks and melting snow were described where salamanders were collected at Peeler Lake. On Half Dome there is a snowfield, the water from which flows over the sheer side and is caught by a strong updraft and blown back on top in a cold, drenching spray. Again, in Tenaya Canyon the gravel was kept wet by melting snow. The ice cone at Yosemite Falls was gone when the specimen was taken there, but spray was furnished in great abundance by the fall. The evidence indicates that high humidity is an important factor in the habitat of *H. platycephalus*.

With the exception of Yosemite Falls and Tenaya Canyon, the localities where Mount Lyell salamanders have been found are all well within the Boreal zones. Habitats of the kind described occur at many localities in these zones between Plumas County to the north and the southern part of Inyo and Tulare counties to the south. It would seem most profitable to look for *Hydromantes* in favorable habitats within these zones, namely the Canadian and Hudsonian life zones.

Cycles of activity.—The Mount Lyell salamander is nocturnal. Of the 45 individuals that I have observed in the field, only two were abroad in the daytime. One was moving about on top of Half Dome in bright sunlight; the other was crawling on a boulder in a dark recess beneath Upper Yosemite Fall. The other 43 animals were under rocks. This is in agreement with the findings of other collectors, for some 28 specimens in the Yosemite Museum taken on Half Dome, presumably in daytime, were found "under rocks in snow water," and the specimens from Sonora Pass were found in the daytime under a rock. The specimen from Silliman Gap was seen actively abroad in the late evening,

and the type specimen and one other with it, were taken at night in a mouse-trap "set in front of a small hole running into the moist soil beneath some rocks." Therefore, it seems that the salamanders remain in seclusion during the day and come out at night.

These salamanders have been found as early as May 1, and as late as August 22. Probably factors of temperature and moisture determine the period of activity. Although the salamanders are out until the latter part of August on Mount Lyell, where the snow lasts until late summer, they may aestivate much earlier on Half Dome, probably when the snow disappears in early July. On September 4, 1938, I spent several hours in fruitless search for salamanders at the base of the Upper Yosemite Fall, where I had found two on my previous visit on July 29. Water was still coming over the fall but the volume had decreased so much that areas which would otherwise have afforded suitable habitats were subject to intervals of drying as the fall was blown back and forth. A period of activity possibly occurs again in autumn when rains increase the volume of water. The salamanders may push farther and farther down into the substrata as their summer environment becomes dry, and then be brought out again by an overabundance of water seeping into their retreats in the autumn and again in the spring.

Food habits.—Remains of the following animals were found in the stomachs of two adult salamanders: 2 centipedes, 8 spiders, 1 termite (*Zoötermopsis nevadensis*), 1 rove beetle (Family Staphylinidae), 6 antlike flower beetles (*Anthicus* sp.), 1 click beetle (Family Elateridae), 1 ladybird beetle (*Hyper-aspis* sp.), 1 leaf beetle (*Diabrotica soror* Lec.), 2 maggots of crane flies (Family Tipulidae), 1 maggot of a fly (Family Muscidae), and 7 adult flies of unidentified species.

A yearling salamander's stomach contained 2 spiders, 3 adult and 19 larval fungus gnats (Family Mycetophilidae), and 1 fly (Family Muscidae).

The stomach of a young-of-the-year contained one Sminthurid (*Sminthurus* sp.), and 10 adult and 11 larval fungus gnats (Family Mycetophilidae).

Most of the food items were ground-dwelling forms, as would be expected in these terrestrial salamanders. The immature salamanders seem more limited than the adults in their choice of food; only small insects and spiders were found in the stomachs of the immature salamanders, which probably cannot capture and swallow the larger insects that constitute the diet of the adults. Small particles of granite were also found in the stomachs.

Size groups.—The 84 salamanders from Half Dome were collected over a period of several years, all between June 14 and 29; they comprise three well-defined size groups (fig. 9 and pl. 22, fig. *a*). The small individuals are probably the young of the year, those of middle size are "yearlings," and those in the largest group are adults. The middle group is smallest because, as Blanchard and Blanchard (1931) have pointed out in a similar study of *Hemidactylium scutatum*, "there has been a year for their numbers to be thinned out by such vicissitudes as enemies, accidents, weather, winter and diseases; and the individuals are more scattered from their year of wanderings." The adult group is largest because it is made up of survivors from the

intermediate groups from an indeterminate number of years; it represents all the survivors of the first two years of growth.

The male secondary sexual characters, enlarged maxillary and premaxillary teeth, may mark sexual maturity. If so, they are a guide to the age at

YOUNG OF THE YEAR
Range: 4.6–5.6
Ave.: 5.1±0.05
Dev.: 0.27±0.04
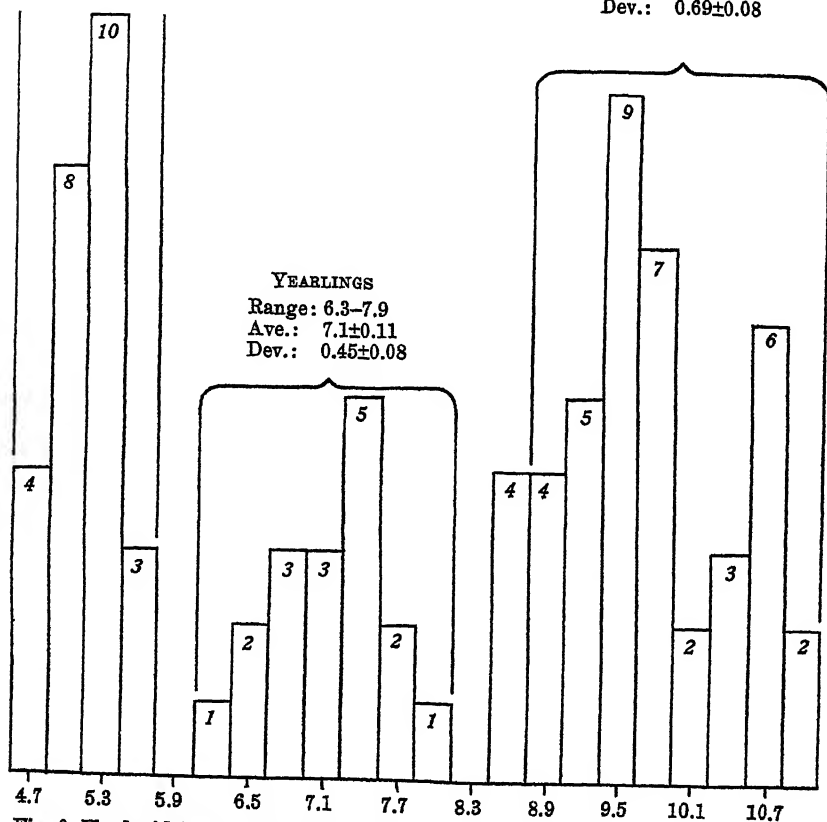
ADULTS
Range: 8.6–11.0
Ave.: 9.7±0.11
Dev.: 0.69±0.08

YEARLINGS
Range: 6.3–7.9
Ave.: 7.1±0.11
Dev.: 0.45±0.08

10   8   4   3   9   7   6   5   4   4   5   3   3   3   2   5   2   3   2   1   2   1   2

4.7   5.3   5.9   6.5   7.1   7.7   8.3   8.9   9.5   10.1   10.7

Fig. 9. Head widths, in millimeters, of salamanders collected on Half Dome. Measurements are grouped into intervals of 0.3 mm.; figures on columns show number of individuals in each class.

which breeding occurs. Although the teeth are absent in the yearlings, they are found in the smallest members of the adult group (8.7 mm. head width), which are judged to be approximately two and a half years of age.

Because the 84 specimens used were taken at the same time each year, the range of size within any one age group is small. Males and females were included in one frequency polygon because the secondary sexual difference in average size (see figs. 1 and 2) is too slight to obscure the grouping by age. A grouping like that based on head width was obtained with the other measurements of total length, head length, body length, and tail length.

SUMMARY

An examination of the skull and all muscles of the head region verifies Dunn's reference of *Spelerpes platycephalus* Camp to the genus *Hydromantes,* and separates it from *H. genei. H. platycephalus* occurs in the Boreal regions of the Sierra Nevada. It is found in granitic soil largely lacking in humus, and is active from the first of May until the last of August, while the soil is kept wet by melting snow. It is nocturnal, its food consisting mostly of ground-dwelling insects, spiders, and centipedes. Specimens from Half Dome collected from July 14 to 29 can be segregated on the basis of size into three age groups : young of the year, animals between one and two years old, and animals more than two years old.

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PLATES

PLATE 21

Fig. *a*. The top of Half Dome, Yosemite National Park, showing habitat of the Mount Lyell salamander; photograph taken April 12, 1939. (Arrow indicates a man at the brink of the sheer face.)

Fig. *b*. Typical habitat on Half Dome, under flat rocks at the foot of a melting snowbank.

a
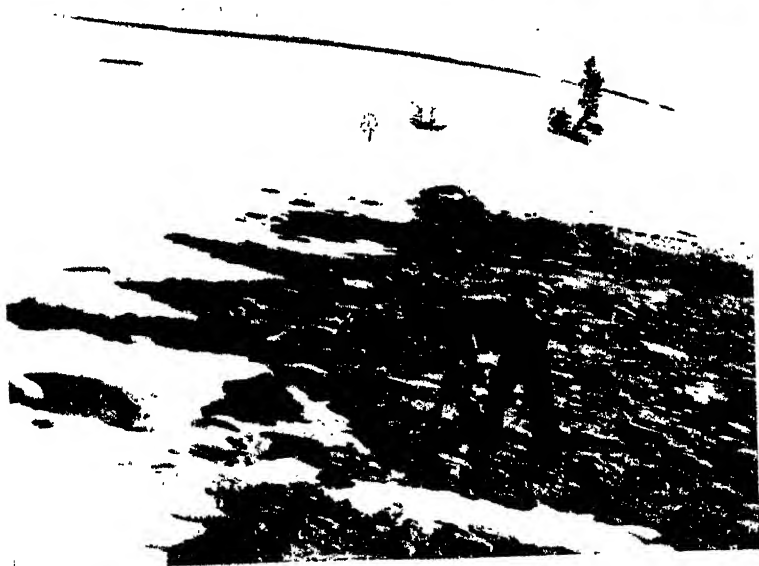
b

PLATE 22

Fig. a. Mount Lyell salamanders. 1. From left to right: small young-of-the-year, yearlings, adult female, and adult male, showing difference in size and head shape of male and female, and of the three size groups.

Fig. b. Live Mount Lyell salamander, male, slightly enlarged. Photo by Ralph Anderson.

a

b

DISTRIBUTION AND VARIATION OF THE HORNED LARKS (OTOCORIS ALPESTRIS) OF WESTERN NORTH AMERICA

BY

WILLIAM H. BEHLE

CONTENTS

DISTRIBUTION AND VARIATION OF THE HORNED LARKS (OTOCORIS ALPESTRIS) OF WESTERN NORTH AMERICA

BY

WILLIAM H. BEHLE

(Contribution from the Museum of Vertebrate Zoölogy of the University of California)

INTRODUCTION

AMONG THE MANY kinds of birds in North America few exhibit such extreme geographic variation as do the horned larks. Thus the species *Otocoris alpestris* has been subdivided by systematists into an extraordinary number of geographic races. Most of the races thus far described show intergradation with their contiguous races. In many of these subspecies, there is geographic variation even within the more or less arbitrary distributional boundaries of each. Few indeed are those races of horned larks that are not further marked by examples of "local variation."

While horned larks are particularly noteworthy as examples of geographic variation, they also show an unusual amount of individual variation. Thus it is a rather common occurrence to find intergradation between neighboring or even between distant races, as a result of the great range of individual variation present.

Besides being exponents of extreme geographic and individual variation, horned larks are possessed of marked sexual dimorphism. The age differences as between juveniles and adults are also pronounced. It can readily be appreciated, then, that horned larks serve as excellent material for the student of variation in the broadest sense of this term.

In addition to the circumstance that horned larks in general constitute especially favorable material for the study of variation and consequently for inquiry into species and race formation, there are certain other considerations that favored the choice of this bird for study. Horned larks are most strikingly differentiated into races in western North America, and in this region there were several problems in the systematics of horned larks that needed attention. There has been no comprehensive study of the distribution and variation of this bird since the revision of the genus *Otocoris* by Oberholser in 1902. Two races have since been described with ranges in, or bordering on, California, where my interests most centered. These were the races *sierrae* and *lamprochroma;* the status of each was doubtful in the minds of students other than their describer. Difficulties were being experienced by systematists in distinguishing between other races of longer standing, between *actia* and *ammophila,* for example. The exact distribution of most races, their areas of intergradation and limits of variation, were more or less obscure. Many examples in collections could not be placed satisfactorily in any of the named races. A revision seemed necessary in order to clear up all these points—or as

many of them as possible—and to analyze critically much of the material accumulated since the review of the species by Oberholser (*op. cit.*) so many years previously.

In undertaking such a revision, however, my main objective was to describe the observed facts of variation as shown by the materials assembled and to correlate these facts, if possible, with physiographic features in the ranges of the individual races. It was felt that pertinent information might thus be gained which would further our knowledge of the factors operative in the process of species formation in this particular bird. As prerequisite to the study of the geographic variation, the variation caused by age, sex, and individuality was given consideration. Molts, plumages, and feather wear were also necessary points of initial attention.

Because of the many factors involved in the great variability of these birds and also because of the practical difficulties in attempting to study them throughout the whole of their range even on this continent, I limited my investigation to the far-western American races, west of the Rocky Mountains and north of Mexico. More explicitly stated, the area of the investigation includes Alaska, Yukon Territory, British Columbia, Washington, Oregon, California, Lower California, Arizona, New Mexico, Utah, Idaho, and Nevada.

Of the numerous races known from North America previous to this investigation, those studied and given full recognition are *arcticola, merrilli, lamprochroma, strigata, sierrae, insularis, rubea, actia, ammophila, enertera, leucansiptila, adusta,* and *occidentalis.* One race, *utahensis,* was described as new in the course of the study. The races known from North America that are not given detailed study here consist of four that are wholly Mexican in their distribution, namely *aphrasta, diaphora, oaxacae,* and *chrysolaema,* and six from central and eastern North America, namely, *alpestris, hoyti, praticola, enthymia, leucolaema,* and *giraudi.* Most of these last-named races were represented in my materials, but only sparsely so. The distributional problems presented by the races *enthymia, leucolaema, praticola,* and *occidentalis* have been by no means cleared up and might well bear intensive study at some later time.

The first systematic work to deal on a relatively large scale with the horned larks of North America was that of Henry W. Henshaw (1884). His main contribution to our knowledge of the geographic variation of these birds was the division of the species into eight subspecies, five of which he described as new at the time. The races that he characterized were *rubea* and *strigata,* from the area I have studied, and *arenicola* (= *leucolaema*), *praticola,* and *giraudi* from elsewhere. In his studies, Henshaw assembled 350 skins. Six years later, Dwight's (1890) publication on the horned larks of North America appeared. He had assembled 2012 skins in the course of his work, on the basis of which material he recognized eleven subspecies, three of them described as new. These were *merrilli, adusta,* and, inadvertently, *pallida* (= *leucansiptila*). Very shortly thereafter, a brief paper by Charles H. Townsend (1890) appeared, in which *insularis* was described as well as the race *pallida.*

By far the most exhaustive systematic study was that of Oberholser (*op.*

cit.), who revised the entire genus *Otocoris*. The number of skins that he examined totaled 2150. In his report, seven new North American races were described, as follows: *arcticola, actia, ammophila, leucansiptila, enthymia, aphrasta,* and *diaphora*. In 1907, Oberholser described the Lower Californian race *enertera*. Ridgway's treatment of the horned larks in his "Birds of North and Middle America," which appeared in 1907, was, for North America, almost the same as that of Oberholser's of 1902. Of recent years, as material has come to hand, Oberholser has described two additional races. These are *sierrae*, in 1920, and *lamprochroma*, in 1932.

Our knowledge of the life history and behavior of horned larks was greatly advanced by Pickwell's outstanding work on the race *praticola* (1931). McAtee (1905) has studied the food habits and economic aspects of horned larks.

MATERIALS AND ACKNOWLEDGMENTS

This investigation was carried on for three years at the Museum of Vertebrate Zoölogy of the University of California. The extensive collection of horned larks in that museum provided the nucleus of materials for the study. These materials were supplemented by skins loaned from the collections of the late Donald R. Dickey, the late J. Eugene Law, Donald D. McLean, James Moffitt, T. T. McCabe, Stanley Jewett, Kenneth Racey, Major Allan Brooks, Randolph Jenks, and Ralph Ellis, as well as by skins borrowed from the Provincial Museum at Victoria, B.C., the Museum of Comparative Zoölogy, the University of Utah, the University of Arizona, the California Academy of Sciences, the Santa Barbara Museum, the Museum of Northern Arizona, and the Natural History Museum at Stanford University. All in all, some 2483 skins were assembled in the course of this study. In September, 1935, I examined the horned larks in the collections of the San Diego Society of Natural History and the Los Angeles Museum of History, Science, and Art. No birds in these two collections were borrowed, however, and none of the data from them has been included here.

To the owners and custodians of the collections mentioned above, I wish to express my appreciation for their aid. I should like also to thank the following people, who have made special effort to obtain horned larks for me from areas from which materials were needed: the late Dr. Joseph Grinnell, Dr. Jean M. Linsdale, Dr. Alden H. Miller, Dr. E. Raymond Hall, Mr. Donald D. McLean, Mr. T. T. McCabe, Dr. Henry S. Fitch, Dr. William B. Davis, Mr. L. Morgan Boyers, Mr. Raymond Gilmore, Mr. Randolph Jenks, Mr. Adrey Borell, and Mr. A. M. Bailey. I wish also to acknowledge the help received under W.P.A. Project 465–03–3–192 in the typing of manuscript and in the making of outline distribution maps.

In spite of the abundance of materials early assembled, skins were lacking from many especially critical areas. I found it necessary, therefore, personally to collect horned larks in southeastern Oregon, northeastern California, Nevada, and Utah. Incidental trips within the past several years have also enabled me to obtain material and to study physiographic features of the ranges of the different races in Oregon, California, Nevada, Utah, and Arizona.

ECOLOGICAL RELATIONSHIPS OF HORNED LARKS

Considered as a whole, the species *Otocoris alpestris* shows an amazing distribution. These birds are found, where the immediate environmental complex is suitable, in almost all of North America. An isolated race occurs in northern South America, in the highlands of Bogota, Colombia. Horned larks are widely distributed in the northern parts of the Old World, being found in northern Russia, Norway and Sweden. Throughout this wide range they are, of course, divided into numerous geographic races.

Horned larks thus occur from the region of the tropics northward to within the Arctic Circle. They are found from sea level to elevations of 12,000 feet. In western North America, horned larks inhabit areas where rainfall is over forty inches per year, as well as arid deserts with but three or four inches of rainfall. One finds them in areas of high atmospheric humidity and in areas of extremely low atmospheric humidity. They frequent open grassy valleys in mountains, or timber-bordered clearings. They occur in stubble fields, in cultivated areas, along roadsides, on vast treeless plains, and in desert wastes.

For most of the subspecies treated in this study, distinctive features are manifest in their respective environments, and the influence of these is more or less evident in the characters of the different races. But within the range of each race, the local occurrence of horned larks seems definitely to be determined by the presence of open country or of barren areas that are comparatively vegetation-free. A certain minimum of vegetation, however, is a requisite of their immediate environment, probably for several reasons. In the first place, horned larks are, to a great degree, graminivorous. Second, various sorts of protection which vegetation affords aid them in withstanding the vicissitudes of weather. In the intense summer heat of desert areas it is a common thing, after the termination of nesting activities, to find individuals, or more often groups, standing in the shade of bushes, fence posts, or trees. In strong winds and in dust storms I have seen horned larks crouch down in short grass and face the wind. In winter storms in the Great Basin these birds seek the protection of Russian-thistle patches or of sagebrush. At times, for instance, when fleeing from winged predators, they find a haven of refuge beneath desert bushes or in rock piles. Bushes, as well as rocks or fence posts, are also a part of the necessary environment during the nesting season, serving as lookouts for the purposes of delimiting and patrolling territory.

Although there is need for some vegetation in the surroundings of horned larks, the point should be emphasized that too much vegetation, like too little, is a limiting factor. There seems to be a narrow range of tolerance with respect to the amount of cover. Pickwell (1931) found, in the course of his observations on individuals of the race *praticola*, that in a single season the growth

and increase in vegetation during the first nesting caused abandonment of the first nest site and the selection of another site in a more open area for the second nesting.

Since horned larks are terrestrial birds, the choice of open country has added significance; this is particularly obvious if one has observed their behavior at large. Horned larks are difficult to approach closely, since they can see an object at great distances. Also, they seem to be ever on the alert. When horned larks are gathered in flocks, the nervousness of one individual often causes a flight of the entire flock, which frequently rises, circles around, and comes down again at a short distance from the original point of departure. Thus, the open country provides a sort of protection for this ground-dwelling bird.

I doubt that horned larks show any preference for surface contour so long as the area is dry and comparatively free of vegetation. Even though horned larks occur and nest in dry areas, without respect to the presence of water, marshy oases in barren areas, or rain pools, or pools from overflowing irrigation ditches often attract flocks of them in the fall of the year. Their active feeding at such pools probably indicates the presence of invertebrate animal life. This is just another of the anomalies in the life of these birds: that they should be so associated, generally, with areas of intense dryness, yet under certain conditions be attracted to wet areas.

Horned larks show certain obvious adaptations to the type of habitat which includes their ecologic niche. The bill of the horned lark is fairly long, slender, and pointed at the tip, thus seemingly adapted for picking up small seeds and grasping small forms of animal life. The circular nostrils are well covered with hairlike feathers, protecting the nasal apertures from the dust which is often so much a part of their environment. The wings are long and pointed, as an aid in powerful flight; these are particularly developed in the male, which indulges at certain times of the year in frequent and prolonged song-flights. The tarsi, toes, and claws are long, a feature presumably correlated with the well-developed capacity for running. When running or walking, these birds appear to take long strides. They have another distinctive habit, mentioned by DuBois (1936:49), of standing with their bodies held as high as possible and their necks and heads stretched upward the better to look about.

Perhaps the most outstanding adaptation is the concealing coloration. Horned larks in general are so colored as to show marked correspondence, at times extremely close, between the color of the dorsum and that of the soil of their particular environment. That this characteristic is manifest in the nestlings and juveniles as well as in the adults seems significant. Juvenal birds have a spotted appearance that is probably of value in concealment. Females are less conspicuous than are males, the less striking color being correlated with the comparatively inconspicuous habits of the female, which assumes the burden of the nesting activities.

Horned larks seem to have few associates and competitors among birds. I have noted vesper sparrows and lark sparrows in horned lark habitat in summer, and lark buntings and snow buntings in winter. Their enemies are certain hawks usually predatory on birds, that is, duck hawk, pigeon hawk, prairie

falcon, and sparrow hawk. Horned larks are preyed upon both in flight and on the ground. Prairie falcons in particular, in the fall and winter, seem to follow flocks about, striking down individuals. Shrikes also take their toll. Ravens sometimes destroy eggs, as do certain snakes. Plowing and harvesting undoubtedly destroy great numbers of eggs and nestlings in cultivated fields. Live stock crush eggs and young in pasture land and open range. Other enemies during the nesting season are weasels, skunks, and ground squirrels. Perhaps the greatest single cause of mortality, as stated by DuBois (*op. cit.*, p. 56), is severe and protracted stormy weather during the nesting season. The death rate from this factor is high among nestlings and juveniles.

Despite the diversity of conditions prevailing in the general range of the species, individual horned larks, local groups, and, to a certain extent, even races seem to be restricted in their habitat relations. During the breeding season, each pair is confined to a circumscribed territory; and even in the fall, when flocking is habitual, certain groups do not seem to wander much. Some entire races are practically resident the year around. Different groups of horned larks are thus subjected to the influence of different sets of local conditions, at least during the critical period of the nesting season, presumably year after year. As a result they seem to have been more or less modified, both morphologically and ecologically, in accordance with each local environment.

MOLTS AND PLUMAGES

With reference to horned larks, Ridgway (1907:297) remarked that "The seasonal and other changes of plumage ... are so marked that it is quite necessary they should be clearly understood by any one attempting the identification of any one of ... the numerous subspecific forms." Dwight (1890) was the first to describe the molts and plumages of horned larks. Among other things he called attention (*op. cit.*, p. 139) to two important facts, first, that only one molt takes place per year, the "breeding plumage" being the single annual plumage with the result of wear upon it; and second, that young birds in their first fall molt replace the wing and tail feathers as well as those of the body.

Since an understanding of molts and plumages is so necessary for working out the relationships of these birds, I felt it wise to verify all preceding statements and assumptions. Dwight worked chiefly with skins of eastern races, and there was the possibility that far-western birds differed in their molts and sequence of feather replacement. Then, too, I was desirous of finding, if possible, some criterion for distinguishing first-year birds from adults.

Although Dwight (1900) stated the sequence of feather replacement for passerines in general, no one to my knowledge had worked out the exact details for horned larks. It was felt advisable to do this for comparative purposes if for nothing else, especially since Alden Miller had recently published his results on shrikes (1928) and on phainopeplas (1933). Accordingly, this molt study was commenced by collecting an extensive series of horned larks during the molting period, August. Birds from Byron Hot Springs, Contra Costa County, California, were referable to the race *actia;* those taken

near Oroville, Butte County, were of the race *rubea*. In late August of the same year, I collected molting individuals of the races *merrilli* and *lamprochroma*. The material thus gathered represented four races. A few skins showing various stages of molt for other races were available in the assembled specimens. Where pertinent material has been available, I have made comparative notes for the different races, particularly with respect to the time of commencement of molt. The material that I collected personally was adequate to show the sequence of feather replacement in both the postjuvenal molt and the annual adult (fall) molt. Thus a basis for comparison of the two was afforded.

Notes on molting birds that I collected were taken in my field notebook before the specimens were made into study skins and while the skins were pliable. The progress of the molt in each bird and the feathers that were old and those that were new or partially grown were particularly observed. This information was later checked on the same skins when dry.

For the sake of completeness and continuity, in the following discussion I will give both the new information on the sequence of feather replacement and the sequence of the molts themselves as demonstrated by my materials.

Sequence of molts.—The natal down is worn for only a few days, whereupon replacement by the juvenal plumage begins. This process is nearly completed by the time the bird has left the nest and started to move about. As so commonly occurs, the natal down is carried out on the tips of the growing juvenal feathers, some of it persisting there for several days, occasionally until the juvenal plumage is almost complete. When the juveniles first leave the nest, they are bobtailed and scarcely able to fly. The juvenal rectrices and remiges continue to grow for several days thereafter.

The juvenal plumage persists for several weeks and is lost by the postjuvenal, or first fall, molt. There may be some correlation between the time of hatching and the time of inception of this molt, for it is well demonstrated by the material at hand that individuals taken on the same day are in different stages of feather replacement. The length of time between hatching and the beginning of the postjuvenal molt I am not able to give. The postjuvenal molt is a complete one, all feathers being replaced by those of the first annual plumage.

There is no definite and regular spring prenuptial molt in horned larks, though a few specimens taken in late February and March show a partial replacement of the yellow throat feathers. Although this is by no means of rare occurrence, it is hardly to be considered as constituting a regular prenuptial molt. Examples showing sporadic prenuptial feather replacement are present from widely scattered localities and at varying dates. A female of the race *strigata,* from Medford, Jackson County, Oregon (no. 65517, Mus. Vert. Zoöl.) taken May 27, 1934, shows feather replacement on the neck. A female of *merrilli* from Gazelle, Siskiyou County, California (no. 67841, Mus. Vert. Zoöl.) taken May 12, 1935, shows similar replacement. Two males, migrants of *lamprochroma,* from Truckee, Nevada County, California, have some new feathers on the throat. These were taken February 18, 1935, and are now.

66891–2, Mus. Vert. Zoöl. These data indicate that the tendency is not restricted to any one race but is purely individual.

Despite the absence of a general prenuptial molt, the breeding plumage is decidedly different in appearance from the fresh fall plumage. The change is due to wear and abrasion of the feathers. The effects are most noticeable on the parts of the body where patches of black feathers are found, on the chest, cheeks, loral regions, and forehead. In fresh plumage, the feathers of these areas are tipped with yellow, which tends to obscure the underlying black. With the wearing off of these delicate tips, the black areas are brought out into bold relief. This phenomenon is, of course, not peculiar to horned larks but is also found in meadowlarks, bobolinks, and other birds. The underlying colors of other areas are similarly brought out by wear. Effects of wear are less noticeable in females than in males, because the black patches are smaller in the former. The nuptial condition of the plumage is attained each succeeding year by a similar process of wear.

Adults have only one complete molt per year, occurring at the end of the breeding season, in the fall; it may thus be termed the annual fall molt or the adult postnuptial molt. In the various series of molting birds that I have collected, some adults which were shot showed a nearly complete molt, whereas other individuals, on the same date, had barely begun their molt. In between these two extremes were representatives of all stages of molt. It seems obvious that there is wide individual variation in the time of inception of the annual fall molt. This, it will be recalled, is comparable to the situation in the postjuvenal molt. Though the individuals in these various stages of molt were all shot from the same flock, it is possible that there is some sort of correlation between time of nesting and time of molt. The intricacies of this correlation have not been explored.

One further point of interest is that, in both juveniles and adults, the sequence of molts is the same in both sexes. This is also true for the sequence of feather replacement in both the postjuvenal and annual fall molt. In winter plumage first-year birds are indistinguishable, as far as I can ascertain, from older ones. For further discussion of this matter, see the section on age differences (p. 217).

Although the first winter and adult winter plumages may be indistinguishable, the juvenal plumage is readily distinguished from the adult. The former lacks any contrastingly colored body areas, such as yellow throat, black chest, and brown back; rather, the whole tone of the juvenal dress is brown, the exact hue varying with the race. Near the ends of the individual juvenal feathers, there are darker areas, and beyond the dark areas, white tips. The white, as it stands out prominently against the dark background, produces a spotted effect over the whole body except on the underparts, which are practically all white, especially the abdomen. The same condition exists on the wing feathers except that the dark brown and white areas are present as bands paralleling the edges.

By way of summary, then, the molt sequence of horned larks shows a postjuvenal molt in which the juvenal plumage is entirely replaced by a first

winter plumage which is indistinguishable from that of the adult. There is no prenuptial molt, but wear produces a breeding plumage that is very different from the fall dress. Adults have an annual molt which is complete, but no regular prenuptial molt.

Postjuvenal Molt or First Fall Molt.—A certain amount of individual variation seems to govern the exact area in which the molt first begins. In general, the process seems to commence simultaneously in several areas, the center of the back, the throat and chin, the marginal wing coverts, and the innermost primary (primary one) and its covert. Corresponding feathers on either side of the body are molted simultaneously, and regeneration is similarly synchronized; in the flight feathers, at least, this may be considered a protective feature, precluding serious impairment of flight.

Following primary one, primary two is replaced and is soon followed by three, four, five, and so forth, in order until the ninth or outer primary is replaced. The replacement of the outer primary is the last stage of the entire molt.

As one flight feather is bursting from its sheath, the next feather in order may drop out, leaving two adjacent spaces without functional feathers. As a rule, however, before one feather drops, the preceding one is a third or more grown. This, too, may be considered an adaptation preventing interference with flight.

About the time that primary five starts to push out of its sheath, the first evidence of molt is to be found among the secondaries. This evidence is the dropping of the ninth, or innermost, secondary and the beginning growth of the adult feather replacing it. Following shortly after secondary nine, number one drops out, and the replacing feather proceeds to grow, keeping at a stage of progress a little behind that of secondary nine though a little ahead of primary number six. Secondary eight follows closely after secondary one and primary six. Next, secondary two is dropped, and following two is seven. The papillae of numbers three and seven become active about the same time. After three and seven are under way, four starts to grow out, then five, and lastly six. There is, then, replacement of the three inner secondaries in the order of nine, eight, seven, proceeding independently of the other six which are replaced in the consecutive order of one to six. We have previously noted that the sequence of replacement of the primaries was from one to nine, that is, from the innermost to the outermost in order. So, from the dividing point between primaries and secondaries the molt of the remiges spreads outward and inward in both directions.

The three proximal secondaries, which molt at a different sequence from the rest, also have a different appearance and for these reasons were called tertiaries by Dwight. As Miller (1928:396) has pointed out in connection with shrikes, these feathers are best designated as secondaries since they are located on the ulna like the others. The term tertiaries is then restricted to an irregular row of feathers along the posterior edge of the humerus.

The upper greater primary coverts are molted at the same time as, or slightly before, their corresponding primaries. This is not true of the greater

secondary coverts, which seem to be entirely replaced before the secondaries start to molt. There is some slight evidence that the greater secondary covert nearest the body is the first of the series to drop; this it does just about the same time that primaries one and two are of good size and number three is emerging from the sheath. Little is indicated by the material at hand with respect to the further order of replacement of the row of upper greater secondary coverts; it is certain, however, that it precedes the molt of the secondaries.

The lesser wing coverts molt shortly after the greater coverts. I have been unable to determine any constancy in the sequence of their replacement. The row of middle coverts molts after the greater and lesser coverts. The first of this series to be replaced is the innermost one, with regeneration continuing in order toward the bend of the wing. The under wing coverts seem to be replaced after the upper coverts are all grown in. The row of marginal coverts is one of the very last feather groups of the entire body to be molted. The feathers of the alula are replaced about the time that primary nine is unfurling from its sheath. Thus the alula is also one of the last areas of feather replacement.

Replacement of the rectrices starts after the replacement of the wing feathers is well under way. Just as corresponding primaries on the two sides drop out at the same time, so do the corresponding tail feathers fall out simultaneously on either side, so that a pair is replaced together. Generally speaking, the replacement of pairs proceeds from the midline to the outside, the outermost pair being molted last. One would expect the innermost pair to molt first, but this does not happen. Without exception, all critical specimens show that the second pair drops first and is followed very shortly by the middle pair, then the third, fourth, fifth, and sixth in the order named. The second pair of rectrices starts to molt just about the time that the first secondary is developing and primary five is pushing out.

The upper tail coverts precede the rectrices in dropping out and seem to be full-grown when the regeneration of the inner three pairs of rectrices is well under way. The under tail coverts follow closely upon the uppers.

Initial areas of molt of the body plumage are several. There seems to be, as already noted, simultaneous appearance of new feathers in the posterior back region, the shoulder and scapular regions, along the femoral tract, and at the sides of the head and chin. The molt spreads throughout the feather tracts from these points. Not all the feathers in one area fall at the same time; instead, there is a differential replacement, some feathers being replaced before their neighbors drop. The main replacement of body plumage commences about the time the fifth primary drops and usually before any of the six distal secondaries are lost. Along with the body molt, the replacement of wing coverts, rectrices, and remiges continues. The last parts of the body plumage to be replaced are the feathers on either side of the body—near where the bend of the wing rests when the folded wing is in place at the side of the body—and along the sides of the neck. Examination of these areas is often useful in determining the age of a bird just before conclusion of the molt.

This study of feather replacement in the postjuvenal molt provides certain proof that all the juvenal rectrices and remiges are entirely replaced—an important confirmation.

Annual fall molt.—With comparative material available, the sequence of feather replacement has also been worked out for this molt. In all essentials, however, it has been found to correspond with the sequence given for the postjuvenal molt.

Geographic variation in time of molt.—Representatives of molting birds have not been available for all the races considered in this paper but the races that are represented agree in all details of molt and order of regeneration. It seems very unlikely that there is any variation among the different races in the sequence of feather replacement in the two molts. Nor is there any indication that the races differ in completeness of molt. Molting examples of the races *actia, rubea, merrilli, lamprochroma, sierrae, utahensis, leucolaema, arcticola,* and *occidentalis* all show that the flight feathers are entirely replaced. In view of the marked geographic variation in color and size exhibited by these races we might have expected some variation in the molt process; but it seems remarkably uniform and stable.

Since horned larks occur from the Arctic tundras to the Sonoran deserts, we might expect variation in the time of molt. Here again we unexpectedly find examples of the race *arcticola* molting at the same, or nearly the same, time as the races in California, Lower California, and Arizona. In addition, horned larks from high altitudes apparently molt as early as do those from lower altitudes.

Although it is a general rule that in the southern, warmer latitudes horned larks nest earlier than they do in the colder regions of the North, it does not follow, as we have seen, that they molt earlier. If there is some sort of general correlation between the nesting cycle and the time of molt—a reasonable assumption—how can this similarity of time of molt be reconciled with the great variation in time of nesting? The probable explanation is that, whereas there is a difference in the earliest nesting dates in the different regions, the time of the close of the nesting season is approximately the same in each race. The reason for this is that the northern races raise but one brood per year, as compared with the two or even three broods in southerly ones. Egg-laying by extreme northern birds probably begins at the time of laying of the third set of eggs in the extreme southern races.

Because of the uniformity of time of molt among the various races studied, we cannot postulate any control through environmental effects except as they regulate the beginning of the nesting cycle. Thus the environment must act indirectly in controlling the time of molt. One further consideration is that the telescoping or shortening of the nesting season among the northern races is bound up to a certain extent with the fall migration. The time of molt is so fixed that feather replacement is completed before migration starts.

In general, it has been found that molt in horned larks takes place somewhat earlier than in most birds. But then, horned larks nest earlier, too, as a general rule. The entire annual cycle is advanced a month or so ahead of that of most

other passerines. The period of molt for horned larks of western North America extends from the middle of June through September, with the period of maximum molt in August. Almost all birds taken in late August or September have been fully molted except for the incomplete growth of certain flight feathers.

ANALYSIS OF VARIATION

Importance of feather deterioration.—Perhaps as important a prerequisite for systematic studies on horned larks as an understanding of molts and plumages, or of individual variation, or of variation with age and sex, is a knowledge of the changes in appearance produced by feather wear and fading. So important are such changes that I venture to predict that the true extent of variability in the plumage coloration of horned larks will not be known until collections are rich in large series of skins in fresh fall plumage taken at the completion of the fall molt and before the individuals have departed from the immediate vicinity of their breeding grounds. Also, it appears likely that, as material in fresh plumage accumulates, the trinominal system of nomenclature will become more and more taxed to express the facts of geographic variation. More and more local variation will come to light, and as this occurs, more and more caution will have to be exercised in the proposing of names. As J. A. Allen (1890:8) said so many years ago, "Very little is gained by naming races distinguishable only by experts, aided by a large amount of material, or where the differentiation is largely a matter of a slight average difference between forms contiguous in habitat . . . ." And further, "Only the exercise of due discretion can prevent the reduction of our 'beneficent system of trinominals' to an absurdity." These statements seem pertinent to the horned-lark problem today.

Sexual variation.—Horned larks, we have said, show rather pronounced sexual dimorphism. Males as compared with females are both larger in linear measurements and heavier in weight. The males are also more highly colored on the occiput, nape, interscapular region, and bend of wing. Their areas of black are more extensive, and the yellow regions as a rule more prominent. The characteristic "horns" on the sides of the head above and back of the eyes, which give the species its name, occur only in the male. Thus, as a result of these differences, the males are much more conspicuous than the females. Notwithstanding all this variation between the two sexes, it is noteworthy that the color of the back is nearly the same in both sexes. This similarity is important from a systematic standpoint.

Individual variation in secondary sexual characters is so great that, occasionally, individual males are found that appear very nearly like members of the opposite sex in the coloration of the occiput, nape, and interscapular region. The reverse is not true, however, for females seem to show less individual variation in certain of their color characters than do males.

The degree of distinction between representatives of the two sexes varies to some extent with the condition of the plumage. There is a closer resemblance in the fall than later, because, after the annual molt, the conspicuous areas of the male are masked by differently colored feather tips. During the breed-

ing season, the greater showiness of the male seems to be correlated with its more conspicuous behavior. In contrast, the female is secretive in action and more concealingly colored.

Variation as a result of age.—Juveniles are decidedly different from both first-year and adult horned larks. The former have a plumage that is characteristically spotted in appearance and of very different texture and color than in postjuvenal birds. It is singular that the coloration of juveniles varies geographically along much the same lines as that of the adults, thus furnishing important aid at times in the diagnosis of subspecies.

As previously noted, the plumages of first-year birds and adults seem indistinguishable, though I have never quite satisfied myself that there are no differences in lengths of rectrices and remiges. Since it is a difficult problem to determine the ages of horned larks that have passed the postjuvenal molt, this similarity of plumages is fortunate for the systematist. The so-called "skull character" is of little value in ascertaining the age of horned larks, for the double-walled condition is invariably present when the birds are still in their juvenal plumage. Horned larks, in my experience, acquire the double-walled skull earlier than any other passerine. In this connection, it is interesting to find that Shufeldt (1883:627) recorded that "perhaps in no species of the highly organized suborder *Oscines* has this almost universal avian feature [of skull bones uniting and sutures entirely disappearing] been so thoroughly carried out."

Since the postjuvenal molt of horned larks is a complete one, there are no feathers retained that are indicative of juvenal plumage. However, the last areas to be molted in both the postjuvenal and adult fall molts are the sides of the head near the gape, the ear region, the sides of the neck, and the sides of the body near where the bend of the wing rests when the wing is folded and held close against the body. Hence, just before the final stages of molt, when the primaries are practically grown out and the body plumage has been almost entirely replaced, there yet remain unmolted feathers in the areas mentioned. The age, therefore, is still indicated when the birds are in almost entirely fresh plumage. It is then possible to compare birds of known first-year and adult ages. This I have done with several series of horned larks collected at the proper time of year, with the result that I am satisfied there are no diagnostic differences in plumage between first-year birds and adults. There does not seem to be any intensification in general color tone in first-year horned larks such as occurs in many other passeriform species.

The problem of whether or not first-year birds differ from adults in length of wing and tail remains unsettled. In all probability, there is no difference, for the postjuvenal molt is complete and the two age categories do not show differences in other characters. Also, there is so much individual variation present in these characters that it would probably obscure any slight differences in wing and tail length resulting from age. Nevertheless, here is a point that needs clearing up.

Geographic variation.—Despite the longstanding employment of the subspecies concept in the systematic treatment of the horned larks, there has been,

I believe, failure to appreciate fully the real nature of the races which have been described. Are these subspecies, which we find replacing each other geographically, the precise units that one judges them to be upon reading the literature pertaining to them? Are there certain natural boundaries delimiting the range of each race? To what extent do the contiguous races intergrade and how large are the areas involved? Are the racial characters constant throughout the range of each race or is there variation within the race? Can the geographically variable horned larks be boxed off into a given number of subspecies and the geographic variation be considered as adequately treated?

That there are subspecies of horned larks seems obvious; but the subspecies are by no means of equal rank. Rather are they of many ranks; they exhibit differentiation in various degrees. Some are distinct and capable of easy definition. Others are rather vague units, weakly differentiated. Some are confined in their distribution to a relatively small area and are quite homogeneous in their characters, whereas others are wide-ranging and widely variable locally. Throughout the range of the species occur many differentiation areas, in which the birds have taken on different characters than are found elsewhere. These centers vary in extent and as a rule are connected with neighboring centers by intermediate populations. In other words, each subspecies has an area where the most typical specimens are found and from which radiate gradients, along whose courses one finds progressively less typical specimens and finally intermediates that illustrate gradual blending into another center.

Although this is the general situation, conditions are often altered by the presence of barriers and consequent separation of stocks. Very often, too, there are trends of variation or gradients running through several races. In certain areas along the gradient one or more characters may be accentuated or new characters appear, the result being that the races appear as steps in a general progression. Also as a part of this situation we find lesser trends within the limits of the subspecies. To present adequately the facts of variation it becomes necessary, then, to point out the center of differentiation for each race and to try to explain the trends between the different racial centers. It is also necessary to discuss the variation within the race in relation to the range of the race. Hence in the following accounts, local variations and areas of intergradation are considered at as great length as materials at command warrant. Boundaries are outlined for the different races, but often it is a matter of individual judgment just where they should be drawn. Such arbitrary action is defensible from a curatorial standpoint, since it aids the arrangement of specimens.

I have stated that not all of the subspecies recognized are of equal rank with respect to the degree of differentiation which they show. Some are barely separable, whereas others are so distinct as to be nearly full species. Yet each race here recognized possesses two prime requisites for being considered a subspecies; these are (1) certain characters or character combinations distinguishing approximately 70 per cent of its representatives from those of other races, and (2) a fairly wide geographic range that permits of relatively accurate definition.

SUBSPECIES ACCOUNTS

Otocoris alpestris arcticola Oberholser

Pallid Horned Lark

Otocoris occidentalis, Baird (1852:318)

[*Otocorys alpestris*] *leucolaema*, Henshaw (1884–258), part

Otocoris alpestris leucolaema, Dwight (1890–142), part; Macoun (1903:362); Coues (1903:507)

Otocoris alpestris arcticola Oberholser (1902:816), original description; Ridgway (1907:307); Macoun and Macoun (1909:393); Osgood (1909:39, 61, 89); Dawson and Bowles (1909:212); Swarth (1922:228); Swarth (1924:347); Brooks and Swarth (1925:75); Taylor (1925:349); Swarth (1926:119); Taverner (1926: 254); Taylor and Shaw (1927:179); Bailey, Brower, and Bishop (1933:34); Taverner (1934:297); McLean (1936:17)

Otocoris alpestris ar[c]ticola, Macoun and Macoun (1915:465)

Chionophilos alpestris arcticola, Hellmayr (1935:2)

Type.—Adult male, no. 78565, U. S. Nat. Mus.; Fort Reliance, Yukon River, Yukon Territory, Canada; May 7, 1879; collected by E. W. Nelson.

Fort Reliance, now in ruins, was an old trading post of the Hudson's Bay Company and was located on the Yukon River a few miles below Dawson. The type specimen probably was not a breeding bird.

Diagnosis.—Size large, as in *Otocoris alpestris hoyti* and *O. alpestris alpestris*, but very much paler than either and lacking their yellow throat and eyestripe; in dorsal color tone, most closely resembling *O. a. lamprochroma* but decidedly larger, throat white, and nape and bend of wing pinker; very much paler than *O. a. merrilli*, larger and lacking yellow on throat; darker and larger than *O. a. utahensis* and without yellow. The combination of large size and entire absence of yellow serves to distinguish this race from almost all other races in North America. In worn plumage, the general color of the back approaches Hair Brown[1] although lighter feather tips give a far from uniform effect. The nape, occiput, and sides of neck are Cinnamon-Drab or Light Cinnamon-Drab, while the bend of the wing is somewhat of an Army Brown. In fresh fall plumage, the central portions of the back feathers vary in color around Fuscous, although the entire dorsum is decidedly streaked because of unworn feather edgings of lighter tone. The nape and occiput regions are less contrasting than in worn plumages.

Measurements (in millimeters).—Breeding males (35 specimens): wing, 109.0 (113.3–103.2); tail, 70.0 (74.4–63.0); bill from nostril, 9.7 (10.9–8.7); tarsus, 22.1 (23.0–21.1); middle toe without claw, 11.2 (12.7–10.2).

Breeding females (14 specimens): wing, 101.9 (104.4–98.4); tail, 63.2 (64.7–61.5); bill from nostril, 9.1 (9.8–8.5); tarsus, 21.6 (22.3–20.6); middle toe without claw, 10.9 (11.6–10.1).

Distribution.—Breeds in interior Alaska, the Yukon Valley and southward at high altitudes through British Columbia and into Washington as far south as Mount Rainier. Winters in the arid interior of British Columbia, in eastern Washington and Oregon, northeastern California, and eastward to Wyoming and Montana.

Specimens examined.—Skins examined belonging to this race totaled 117, classified as follows: breeding males, 47; breeding females, 21; autumn and winter males, 26; autumn and winter females, 11; juveniles, 12. Localities represented are as follows. Unless otherwise stated, the skins are in the Museum of Vertebrate Zoölogy. Breeding localities are indicated by an asterisk.

ALASKA. Mountain between Savage and Sanctuary rivers, 5000 feet. Mt. McKinley District*, 1; Ewe Creek, 2800 feet, Mt. McKinley District*, 2; Dry Creek, 3000 feet, Mt. McKinley District*, 1.

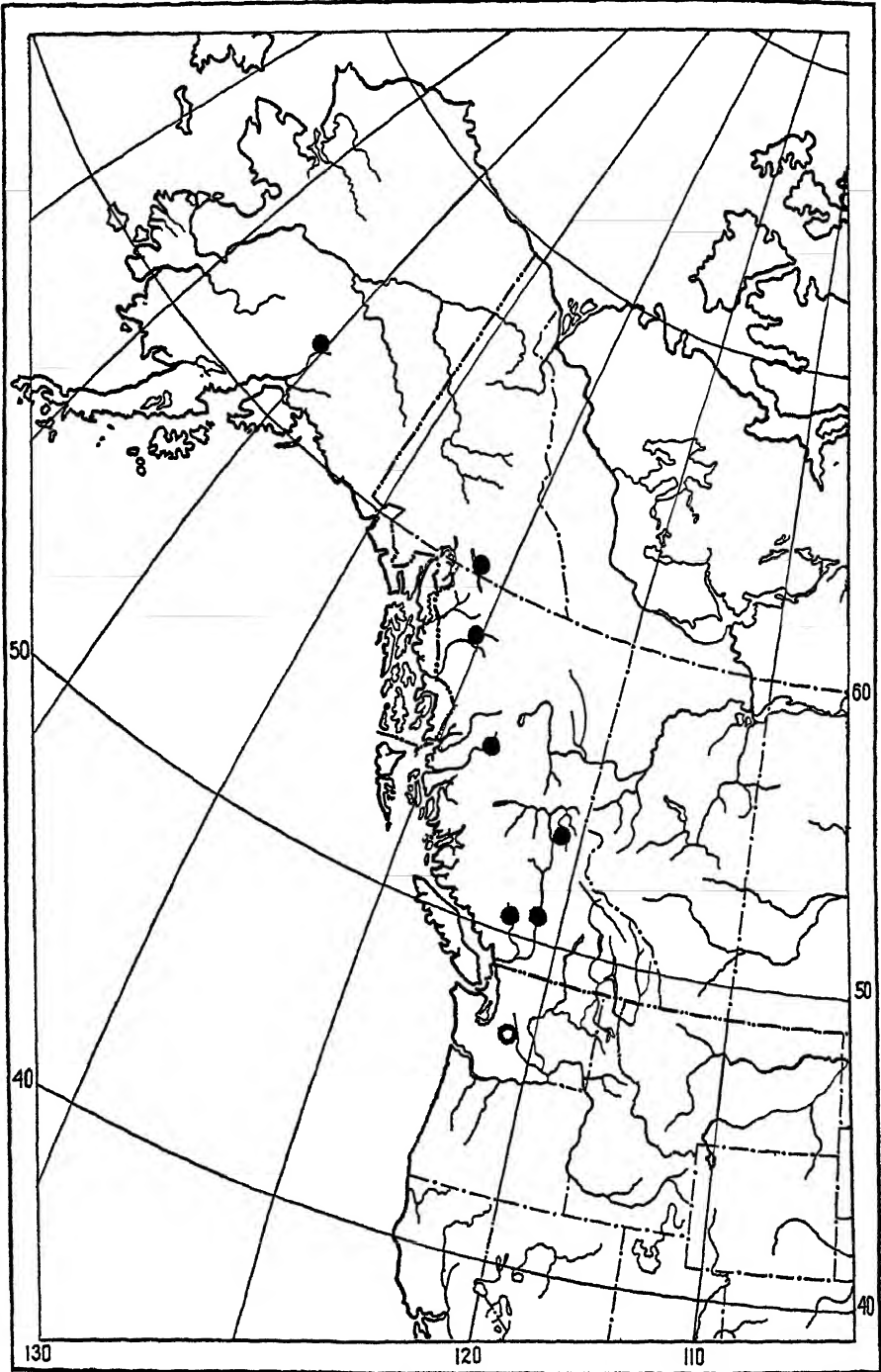[1] Names of colors capitalized are those of Ridgway (1912).

Fig. 1. Map showing the distribution of the race *Otocoris alpestris arcticola.* Dots indicate localities from which breeding specimens have been examined. Circle represents published breeding record.

YUKON. Forty Mile, 1.

BRITISH COLUMBIA. Shore of Lake Atlin, 3 (Calif. Acad. Sci.); Monarch Mt., near Atlin*, 4; Monarch Mt., 5 mi. S Atlin*, 4 (Calif. Acad. Sci.); Gopher Dam Mt., Atlin*, 3 (Provincial Mus.); Wilson Creek, 5000 feet, Atlin*, 9 (Provincial Mus.); Spruce Mt., 15 mi. E Atlin*, 7 (Calif. Acad. Sci.); Spruce Mt., 20 mi. E Atlin*, 10; mountain, 4500 feet, above Doch-da-on Creek, Stikine River*, 4; mountain above Fourth-of-July Creek*, 1 (Calif. Acad. Sci.); mountain south of Blue Canyon*, 5200 feet, 2 (Calif. Acad. Sci.); Nine-mile Mt., NE Hazelton*, 3; Rainbow Mountains*, 14 (McCabe coll.); Indianpoint Lake*, 3 (McCabe coll.); 100-Mile House, 3 (McCabe coll.); 10 mi. E Hanceville, 3 (McCabe coll.); Itcha Mt., 6000 feet, Chilcootin, 2 (Racey coll.); Tenquille Lake, Finch Mt., Pemberton*, 1 (Racey, coll.); Kamloops, 6 (Racey coll.); Okanagan Landing, 7 (Mus. Vert. Zoöl.), and 6 (Provincial Mus.); Lillooet*, 6 (Provincial Mus.); Sicamous, 1 (Provincial Mus); Overlord Mt., Mons, 1 (Racey coll.); London Mt., 6200 feet, Mons, 1 (Racey coll.); Mt. Whistler, 7000 feet, Alta Lake*, 4 (Racey coll.); Red Mt., Alta Lake*, 1 (Racey coll.); Osooyos, 1 (Provincial Mus.); Victoria, 1 (Provincial Mus.); Sumas Lake, 1 (Provincial Mus.).

CALIFORNIA. Lassen County: 2 mi. S Reno junction on Reno-Susanville Highway, 1 (McLean coll.).

Habitat notes.—Members of the race *arcticola* seem to be found breeding only where arctic-alpine conditions prevail, which is normally above timber line. Thus they are encountered at comparatively low elevations in the northern part of their range and at higher altitudes on isolated mountaintops in the southern part. Swarth (1924:319) describes their breeding home on Nine-mile Mountain in the Skeena River region, British Columbia, as follows: "The country above timber line, covering many miles along the higher ridges, is open and park-like. . . . White fir and mountain hemlock (*Tsuga mertensiana*) occur, dwarfed and prostrate, forming scattered thickets over ground that otherwise is mostly grass covered. Snow banks persist through the summer, and below the melting snow are occasional little lakes, sometimes an acre or more in extent. On damp slopes grass is replaced by false heather (*Cassiope mertensiana*), luxuriant growths that cover extensive areas. Below the ridges the grass became much higher and was intermingled with lupine." Under similar conditions above timber line on the treeless mountain summits, Swarth found horned larks of this race on open, moss-covered slopes. In the same life zone and under these same general conditions, ptarmigan, rosy finches, and pipits were found.

Taylor (1925:351) presents the following picture of their habitat in the southern part of their range at Mount Rainier, Washington: " . . . the landscape was practically always wind-swept; the vegetation, while sometimes making a grassy sward of not a little attractiveness, was usually sparse and often depauperate; the ground was often extremely rocky and poor; and trees, when present at all, were the dwarfed and gnarled types of the timber-line region."

According to Major Allan Brooks, in the mountains of Canada the higher, barren, wind-swept slopes become free of snow in the spring long before the valleys and flats. On these upper slopes, the horned larks are able to nest comparatively early. Even so, there is apparently a hastening of the nesting season, resulting in the completion of the nesting cycle before the onset of

unfavorable conditions. This is indicated by the following data. Several birds taken by T. T. McCabe on May 2, at the 100-Mile House, British Columbia, were not on their breeding grounds but rather were in lowland territory where *merrilli* breeds. According to the collector's notes, the gonads of these birds did not show any great enlargement. Also in the McCabe collection are five females and several males taken June 20 in the Rainbow Mountains, British Columbia. According to label data, four of these females had brood patches, and the ova were very small. The fifth female weighed about two grams heavier than the others; the largest ovum was 10.0 mm. in diameter, and there was no brood patch. It would seem, then, that the nesting takes place in early June.

Most of the juveniles of this race are of July dates, although one taken in the Mount McKinley district is of date June 12. The annual molt commences as early as August 1, judging by the material at hand. This, incidentally, is approximately the time that the more southern races in California start their molt. Osgood (1909:39) noted that in Alaska the birds were beginning to flock by late August. Munro (1931:21) has recorded that his earliest date for their arrival in the lowlands at Okanagan Landing, British Columbia, was November 13. It is likely, then, that but one brood of young is raised per season. The whole sequence through the nesting cycle seems to be adapted to conditions of the summer habitat.

In addition to the adaptive synchronism of the nesting cycle with the arctic-alpine climatic conditions, another habitat feature deserves mention. This has to do with the condition of continuous wind. McCabe found a nest on a ridge at Indianpoint Mountain, British Columbia, where the wind was blowing incessantly, yet the horned larks seemed little affected. Osgood (*op. cit.*, p. 89) remarked that his party collected three specimens of the Pallid Horned Lark on September 4 in the Russell Mountains of the Macmillan Range in Alaska. A high wind was blowing at the time but the horned larks evidenced no desire to keep on the lee side of the mountain. In my own experience, members of the races *actia, lamprochroma, utahensis,* and others, seek protection under similar circumstances, usually by crouching down in short grass and facing the wind. It may be that the larger build and greater wing length of members of the race *arcticola* are as much correlated with their windy habitat as with their migratory habit.

Distribution and variation.—Originally this race was thought to breed only in interior Alaska and Yukon Valley. Field work by Brooks, Swarth, and others in recent years has shown, however, that it also breeds above timber line in the mountains of British Columbia. Taylor (1925) ascertained this fact for the higher peaks of the Cascade Range in northern Washington. The Pacific Coast strip of Alaska is generally omitted from definitions of the range but the race may well occupy mountaintops right up to the sea front. Swarth (1922:228) found Pallid Horned Larks breeding in small numbers on mountaintops above Doch-da-on Creek in the Stikine River region of central British Columbia, a locality but sixty miles from the coast. Of the region nearer the sea, he said, "From the mountain we were on, however, we could see many similar peaks and ridges far to the westward, where the species would

probably be found could these summits be reached." A few lines later he states: "Horned larks may well occur at favorable points but a few miles back from the coast, but the circumstances are such that it is doubtful if this possible habitat will soon be invaded by any collector."

As a result of the restriction of *arcticola* to a boreal habitat, we find in certain parts of its range a most interesting zonal relationship with *merrilli*. In the more northern part of its range (Alaska, Yukon, and extreme northern British Columbia) *arcticola* is apparently the only form of horned lark existing; but in the southern part of the geographic range, we find *merrilli* also. However, the two races are there well separated ecologically. Whereas *arcticola* occupies meadows or rocky ridges above timber line and is truly a mountain or highland form, *merrilli* is found at lower altitudes and is essentially a lowland form. Each race thus occupies a different zone with included ecologic niche, with different plant and animal associates. The result is complete separation of the two races during the breeding season and, in consequence, a lack of intergradation through interbreeding. It is significant that overlapping of characters through individual variations appears to be absent.

It probably is not unusual to find areas where breeding birds of the two races are separated vertically by only a few thousand feet. This doubtless occurs in the state of Washington, in the vicinity of Mount Baker, Chopaka Mountain, and Mount Rainier, where *merrilli* occurs in open areas at the bases of the mountains and *arcticola* probably breeds near the top. Brooks (1909:62) mentions just such a separation for the Okanagan region, British Columbia. Speaking of *arcticola*, he states: "This is the breeding form on all the high mountains of the Province, *Otocoris a. merrilli* being restricted to the arid lower levels; nowhere do their breeding ranges impinge on each other." This is not unlike the separation to be noted later with respect to the races *sierrae* and *lamprochroma;* these two races, however, do intergrade in places where physical features permit, and thus the separation between the two is not nearly as complete as between *merrilli* and *arcticola*.

What the relationships are between *arcticola* and *hoyti* I am not prepared to say. However, considering the relation between *arcticola* and *merrilli*, intergradation by contact cannot be assumed until actual proof of such intergradation exists. Oberholser indicates that such intergradation does occur, for he has recorded (1902:814) that the series upon which Dr. Bishop based his description of *hoyti* (spring specimens from Towner County, North Dakota) are in large proportion intermediates in various degrees between *hoyti* and *arcticola*. He further states that the type of *hoyti* is, itself, one of these intermediate specimens. Even if *arcticola* proves to be as distinct from *hoyti* as it is from *merrilli*, the use of the trinominal best expresses the relationships of *arcticola* to other races and is quite in keeping with practices among systematists in handling similar relationships elsewhere. The geographically isolated *O. a. peregrina* in South America is treated trinominally even though its nearest neighbor is in southern Mexico.

The race *arcticola* differs from most of the other races in one other respect. This is the fact that very little geographic variation is displayed within the
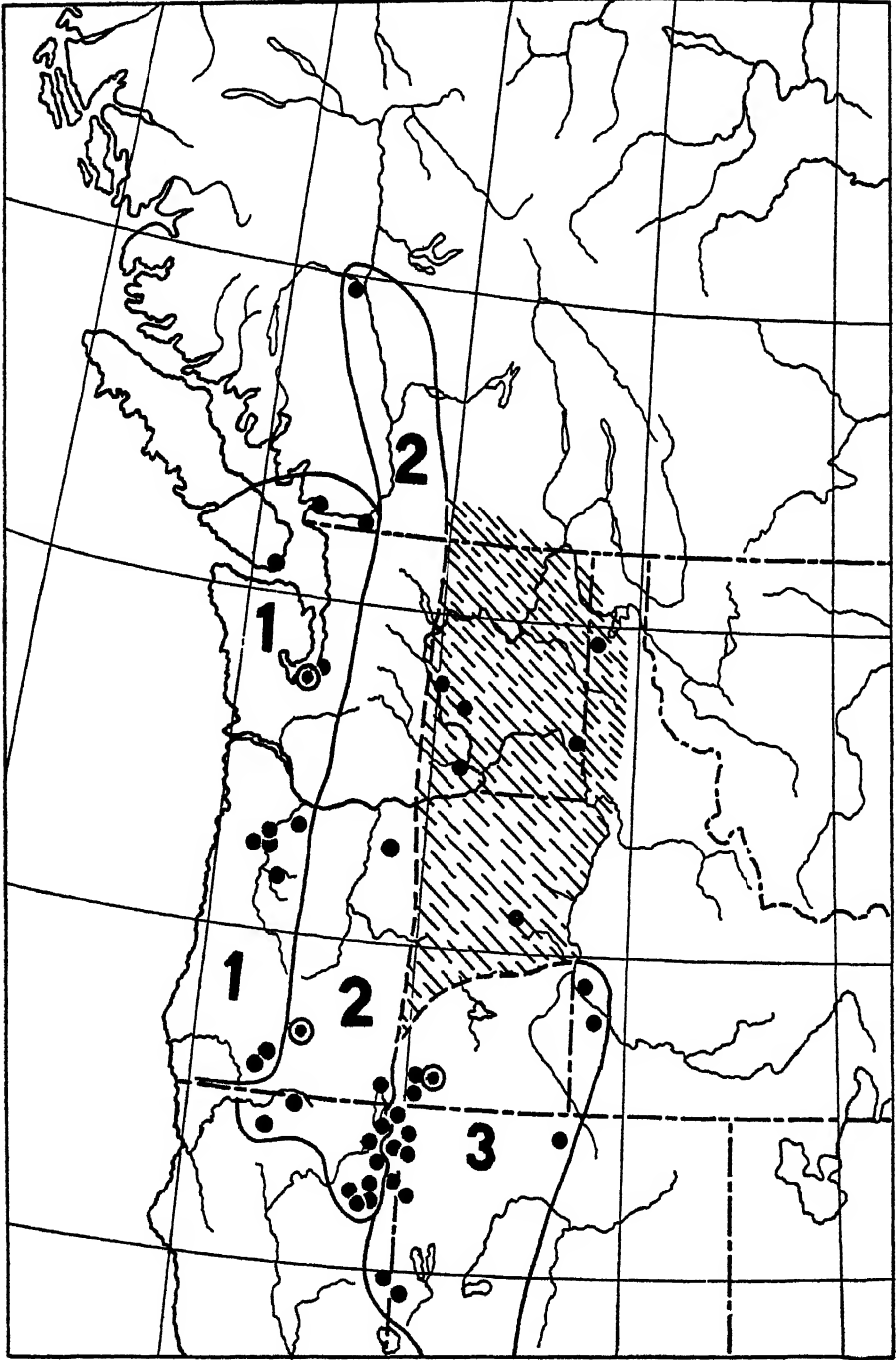
Fig. 2. Map of central western North America outlining breeding ranges of: 1, *O. a. strigata*; 2, *O. a. merrilli*; 3, *O. a. lamprochroma*. Plain dots indicate breeding localities from which specimens have been examined; encircled dots show type localities; zone of intergradation indicated by shading.

race. I have been able to detect in my materials no special trends in the variable characters, nor any local peculiarities among breeding birds. Even the winter-taken examples present a singular uniformity of appearance as compared with other races, which display so much local variation. Individual variation is also less marked in *arcticola* than among other races. Oberholser evidently found similar conditions in his material for he remarked (1902:817), "The breeding specimens available are quite uniform, with the exception of a male from St. Michael, Alaska, which is noticeably more reddish on the upper parts. Even in winter there seems to be less individual variation than exists in many of the other subspecies." The juveniles of this race have the distinction of being the blackest of those in any of the races studied.

Otocoris alpestris merrilli Dwight

Dusky Horned Lark

[*Otocorys alpestris*] *arenicola* Henshaw (1884:259), part
Otocoris alpestris strigata, Merrill (1888:259)
Otocoris alpestris merrilli Dwight (1890:153), part, original description; Belding
   (1890:106); Bendire (1895:346); Merriam (1899:118); Oberholser (1902:833),
   part; Grinnell (1902:44), part; Macoun (1903:368); Ridgway (1907:315), part;
   Macoun and Macoun (1909:401); Grinnell (1912:15); Grinnell (1915:95);
   Macoun and Macoun (1915:474); Mailliard (1921:92); Mailliard (1923:18);
   Dawson (1923:840), part; Taverner (1926:254); Grinnell, Dixon, and Linsdale
   (1930:285), part; Bangs (1930:366); Grinnell (1932:285); Taverner (1934:297)
Eremophila alpestris merrilli, Bangs (1930:366)
Chionophilos alpestris merrilli, Hellmayr (1935:6)

Type.—Adult male, no. 219516, Mus. Comp. Zoöl. (no. 19516 William Brewster collection); Fort Klamath, Klamath County, Oregon; July 1, 1887; collected by Dr. J. C. Merrill.

When Dwight (1890:153) presented his diagnosis of the race, no type was designated. Instead, he described each of five representative skins taken at Fort Klamath, a male and a female in breeding plumage, a male and a female in winter plumage, and a juvenile. Oberholser (1902:833) designated the adult breeding male as type (lectotype). In this practice he was followed by Ridgway (1907:315). Bangs (1930:366) has listed these five specimens as cotypes, refusing to recognize any single one of them as a holotype.

Diagnosis.—Darkest of all the races when in typical form; more blackish than *strigata*, larger, and lacking the yellow below; same size as *lamprochroma* but darker and more blackish; also similar in size to *sierrae* but lacking the reddish brown of the latter as well as the yellow below; distinguished from *arcticola* by smaller size, darker dorsum, and yellow chin and throat. Color of dorsum in fresh plumage somewhat near Blackish Brown (3), wearing and fading to Clove Brown. Occipital region, nape, sides of neck, and bend of wing Army Brown in unfaded condition.

Measurements (in millimeters).—Breeding males (49 specimens): wing, 101.0 (105.0–94.2); tail, 68.2 (74.0–61.7); bill from nostril, 9.4 (10.4–8.3); tarsus, 21.0 (22.0–19.8); middle toe without claw, 10.4 (11.5–9.6).

Breeding females (17 specimens): wing, 93.8 (96.7–91.3); tail, 60.5 (63.4–57.0); bill from nostril, 8.7 (10.1–8.2); tarsus, 20.5 (21.8–19.2); middle toe without claw, 10.3 (11.8–8.8).

Distribution.—Breeds in suitable open country on the east slope of the Cascade Range and in lowland plains east of the mountains from the Chilcotin Plateau of central British Columbia south through Washington and Oregon to central northern California and northeastern California west of the Warner Mountains. Winters, in part, in eastern Washington, Oregon, and California, and also in the Sacramento Valley in California. A few individuals possibly winter along the coast strip of Washington and Oregon.

Specimens examined.—Skins referable to this race totaled 198. Of these, 55 were breeding males, 26 breeding females, 73 autumn and winter males, 21 autumn and winter females, and 23 juveniles. These came from the following localities. Breeding localities are marked with an asterisk. Unless otherwise indicated the specimens are in the Museum of Vertebrate Zoölogy.

BRITISH COLUMBIA. Riske Creek P. O., Chilcotin Plateau*, 11 (McCabe coll.), 2 (Racey coll.); Okanagan Landing, 6 (Racey coll.), 1 (Mus. Vert. Zoöl.).

WASHINGTON. Benton County: Kiona, 2 (Jewett coll.).

OREGON. Tillamook County: Netarts, 1 (Dickey coll.). Wasco County: 5 mi. N. Shaniko⁺, 1 (Santa Barbara Mus.). Morrow County: Cecil, 5 (Jewett coll.). Sherman County: Grass Valley, 1 (Jewett coll.). Klamath County: Fort Klamath*, 35 (Mus. Comp. Zoöl.), 2 (Mus. Vert. Zoöl.). Lake County: 7 and 8 mi. W Lakeview, 21.

CALIFORNIA. Siskiyou County: Yreka*, 27 (Calif. Acad. Sci.); Klamath Pass, 1 mi. S California-Oregon border, 2; 3 mi. N Montague*, 3 (McLean coll.); 3 mi. NW Gazelle*, 4. Modoc County: Davis Creek*, 2 (Moffitt coll.); Alturas*, 9 (Mus. Vert. Zoöl.), 1 (Santa Barbara Mus.); Steele Meadow, 1; 5 mi. S Likely, 7. Lassen County: Grasshopper Valley⁺, 2 (McLean coll.), 1 (Santa Barbara Mus.); mouth of Bailey Creek on west side Madeline Plains*, 1 (McLean coll.); Madeline, 1 (Calif. Acad. Sci.); Termo, 1 (McLean coll.); 2 mi. S Termo*, 1 (Santa Barbara Mus.); Ravendale, 4; 7 mi. S Ravendale*, 3 (Santa Barbara Mus.); Horse Lake*, 5 (Mus. Vert. Zoöl.), 1 (McLean coll.), 7 (Mailliard coll.); Jones'*, 1; Petes Valley*, 4; 3 mi. N Standish, Honey Lake Valley, 3 (McLean coll.); Champ's Flat on Pine Creek, 1. Butte County: 1½ mi. S Oroville Junction, 1 (McLean coll.); Gridley, 2 (Mailliard coll.). Glenn County: 3 mi. E Norman, 6. Sonoma County: Cotati, 5 (Mailliard coll.). Stanislaus County: Modesto, 4 (Mailliard coll.).

Habitat notes.—Unlike *arcticola,* which has relatively uniform environmental conditions, *merrilli* occurs in areas that show considerable diversity of habitat. The type locality well illustrates the nature of the physical conditions of the race in the Cascade Range.

Fort Klamath is situated at an elevation of 4,250 feet in the upper or northern end of a small valley some twenty miles long and seven miles wide on the east side of the crest of the Cascades. The valley is flanked by growths of coniferous trees, such as the lodgepole pine (*Pinus contorta*), yellow pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga taxifolia*), and Engelmann spruce (*Picea engelmanni*). There is also some juniper. The valley floor is damp and rather marshy in places. Occasionally, there are dry fields with only scattered vegetation, and it is in such places that horned larks of this race nest. Dr. J. C. Merrill, who collected the type specimens in 1887, found horned larks to be scarce and local in their distribution. He states (1888) that they were found in the latter part of March in a wet meadow, which later in the season became dry, bordering a marsh. He further states (*op. cit.,* p. 259), "Here there are many little ridges rising a foot or two above the general level and but a few feet in width; the tops were, however, dry and in many places bare; to these the Larks were closely confined, each pair having its own limited range."

To the southward, in Shasta Valley, Siskiyou County, California, and in northeastern California, members of this race occur on open, treeless, undulating plains where the shrubby vegetation is sparse, consisting chiefly of sagebrush. In central Washington, the habitat of horned larks probably nearest this race is said by Dice (1916:307) to be bunchgrass in open prairie country.

The breeding range of *merrilli* is subject to rather severe winters, and the race as a whole is migratory. All individuals, however, do not necessarily leave the breeding range. Some information is at hand on the migration dates of this race. A series of specimens taken by Kenneth Racey on March 4, 1926, at Okanagan Landing, B.C., evidently were among the first to return to their breeding grounds. Data noted on the labels of the study skins indicate that at the time these birds were shot the gonads had already increased to a considerable size. The testes ranged from about 3 to 8 mm. in length. There is little doubt that these specimens represented the breeding birds of the region. However, several examples taken from February 21 to February 27, 1923, on their wintering grounds near Norman, Glenn County, California, showed only initial gonad swelling and were exceedingly fat. At this time individuals were in flocks of a dozen to twenty (Grinnell, 1923:172), whereas members of the resident race *rubea* were widely distributed in pairs and the males were performing their song flights.

The winter representatives of *merrilli* from the Sacramento Valley closely resemble breeding birds from Montague, Siskiyou County, and from Fort Klamath. In all probability, birds from central southern Oregon and central northern California winter in the Sacramento Valley, while those from the Madeline Plains region of northeastern California probably winter chiefly in the Honey Lake Valley. Individuals from British Columbia and the Cascade Range proper probably winter in eastern Washington and Oregon along the Columbia River or farther south. A few from British Columbia and Washington may pass through the Fraser River and Columbia River gaps and winter on the west side of the Cascade Range.

Dice (1918:148) records a juvenile on April 10, 1905, near Prescott, Washington; it was just able to fly. On April 18 of the same year, he found a nest with three eggs. The following year, on April 12, a nest with three partly feathered young was noted. In 1908, nests with two and three eggs were found on March 27, and on April 7 a young bird fully feathered and able to fly was found. Merrill (1888:259), in the relatively late season of 1887, took a female on May 23 that contained an egg almost ready for extrusion; another female had already deposited her eggs and was incubating. On June 17, he found a nest containing three young about five days old, and on July 1, he shot a female that contained two eggs, one of which was almost ready for extrusion. D. D. McLean found young just able to fly in Shasta Valley on April 6, 1936. Thus, it would seem that members of the race return to their breeding grounds by the first week in March and some commence laying by the last week in March. Two broods are probably reared per season.

Distribution and variation.—The description of the race *sierrae* from the northern Sierra Nevada in California and the later description of *lamprochroma* from western Nevada and southeastern Oregon made necessary comparative examination of topotypical material of the races *merrilli, sierrae,* and *lamprochroma.* Such examination has revealed that all three races are tenable. *Merrilli,* despite the restriction of range as a result of the description of *sierrae* and *lamprochroma,* still presents within its range many instances

of local variation, with attendant problems of distribution, a discussion of which follows.

In typical form, *merrilli* is the blackest race of horned lark in North America. Examples from the type locality are not altogether typical though they show an unusual amount of purely individual variation. This individual variation is most noticeable in the color of the nape, which varies from dull vinaceous to a bright ruddy. The dorsal tone on some examples tends toward ruddy brown; others display more of blackish. The juvenal examples from Fort Klamath are also very variable. Of the seven examined, four represented the brown extreme, whereas three were more blackish.

Examples of the race closely similar to those from Fort Klamath have been examined from Lakeview, Lake County, Oregon, and from other localities south to Alturas, Modoc County, and the Madeline Plains in Lassen County, California. The blackest birds, both of breeding specimens and of those in fresh fall plumage, come from these localities.

In northeastern California, *merrilli* comes in contact with the races *sierrae* and *lamprochroma;* here, topographical features seem to determine the distribution of these three races. The Warner Mountains throughout their length apparently separate the ranges of *merrilli* and *lamprochroma*. No representatives are at hand from immediately north of these mountains; but at their southern end the two races appear to intergrade. As indicative of this, breeding examples from Observation Peak, Lassen County, California, are referable to *lamprochroma*. A male from Jones', a locality a little to the northeast of Observation Peak, seems closest to *merrilli*. Still farther to the north, at Red Rock, a male was taken which seems intermediate between the two. Of three breeding males taken 7 miles south of Ravendale, two are fairly typical of *merrilli* but the third shows an approach to *lamprochroma*. A single breeding male from Horse Lake is an intergrade between *lamprochroma* and *merrilli;* but from Petes Valley to the south are two males in worn plumage that are closest to *merrilli*. One male from 6 miles north of Wendel is closest to *lamprochroma*, yet it was taken in practically the same valley as the Petes Valley specimen. Some of these last-named males may have been wanderers at the close of the nesting season and hence not on their breeding territories when collected. This is probably true of those from Petes Valley and Jones', which were taken in late July. Several autumn examples from the general region of racial contact are also intermediates; so there is strong evidence that *merrilli* and *lamprochroma* do intergrade in Lassen County north of Honey Lake and between Eagle Lake and the Nevada-California boundary. This area of intergradation is of limited extent, though, as compared with intergradational areas elsewhere between other races.

No examples of breeding birds are present that might be considered as intergrades between *merrilli* and *sierrae*. Belief that there may be intergradation between these two races is based on the presence of nontypical fall or winter examples of *sierrae* (discussed under that race) that seem to approach either *merrilli* or *lamprochroma*. If intergradation between *merrilli* and *sierrae* does occur, the most likely place for it would be east of the north end of Eagle Lake

or in the Fall River Valley. The nature of the country west of Eagle Lake and thence north, with its dense forest and few clearings, makes intergradation there extremely doubtful. Examples of breeding birds in Grasshopper Valley are typical of *merrilli* and show no evidence of intergradation with *sierrae*.

Merrilli does not come into contact at all with *rubea* in the Sacramento Valley of California. The two races are widely separated, except in winter, by a barrier of timber and mountains.

A most unusual instance of local variation has come to light in specimens from Shasta Valley, Siskiyou County, California. This local peculiarity occurs in the vicinity of Yreka and is fraught with significance. In the same valley and only a few miles apart, under the same climatic conditions and with no apparent physical barrier present, we have indications of strikingly different populations. Three breeding males taken April 6, 1936, three miles north of Montague are quite blackish and are almost identical with many of the Fort Klamath examples, as well as with those from the Madeline Plains. Three other males from an area three miles northwest of Gazelle are somewhat browner, lacking the blackish appearance. They were collected May 12, 1935. Then there is also a large series of breeding males and females, together with many juveniles from Yreka, some taken June 6, 1920, others June 8, 1922. All specimens from Yreka are uniformly dark brown. To repeat, the three localities mentioned are all in the same valley, Shasta Valley, and only a few miles apart. Yet the samples from the three populations exhibit a range of variation that is greater in amount than the differences between some races.

The differences manifest among the examples from this one valley cannot be attributed to any adventitious coloring, or to age or sex differences. It seems as though the populations differ genetically in their characters. The skins from Yreka are not only browner but also more yellowish than those from Montague. The yellow pervades the sides of the head and covers the auriculars. This can scarcely be explained by adventitious coloring or pigment change. It is to be noted further that the skins were taken in different years. Just how these divergencies may have arisen is a problem.

The brown Yreka examples show a closer resemblance to horned larks from Medford, Jackson County, Oregon, on the west side of the crest of the Cascade Mountains, than they do to topotypical examples of *merrilli* from Fort Klamath on the east side of the Cascade Range. On the other hand, the skins from Montague are the same in appearance as those from Fort Klamath. Yreka and Medford are far distant geographically, and mountainous country lies between the two localities. Still, the possibility exists that the Yreka population may have originated from the Medford *strigata* stock. But the Yreka locality is in what may be considered as *merrilli* territory, and examples of the latter race even breed in the valley, at Montague, where they are immediate neighbors of the Yreka population. If this were simply an instance of intergradation, one would expect less uniformity among specimens from one locality or a blending of two populations. The Gazelle specimens, though, are somewhat intermediate between the Yreka and Montague representatives. That these observed facts can be interpreted at present as evidence of intergradation

between *merrilli* and *strigata* is doubtful. The fact remains, however, that the southernmost examples of *strigata* tend to become larger and more brownish (less blackish), and so to resemble those from Yreka.

One possible explanation for this fact is that horned larks from both *strigata* and *merrilli* stocks have reached the valley very recently and that, to date, the groups of independent origin have kept pretty much apart. However, considering the marked uniformity of each population, it seems more reasonable to postulate that some form of isolation or some environmental difference in the valley has been responsible in one way or another for the differing populations. Locally different populations have been found time and again in horned larks but never have I found them to be so marked or so closely situated as in the present instance. From a taxonomic standpoint, specimens from all parts of the Shasta Valley are, for the present at least, to be called *merrilli*, even though some are aberrant.

Although examples from the most northern part of the range of *merrilli* are almost exactly like those from the southern part of the range in California, little is known of the geographically intermediate populations. Between Fort Klamath, Oregon, and Okanagan Landing, British Columbia, only one breeding example of true *merrilli* has been available. This is a male taken near Shaniko, Wasco County, Oregon. It is black, like typical specimens of *merrilli*. East and northeast of this locality, along the Columbia River, all representatives at hand are perceptibly browner than typical *merrilli* and have ruddier napes. This probably indicates a blending of *merrilli* and *lamprochroma*. It is a question whether to call these examples *merrilli* or *lamprochroma,* for they are typical of neither. I believe they are closer to *lamprochroma* than to *merrilli,* hence I have discussed them under *lamprochroma.* In this connection it should be recalled that Oberholser (1902:838), in speaking of *strigata,* stated that "breeding specimens from both sides of the Columbia River in the vicinity of The Dalles, Oregon, approach *merrilli,* but are smaller and less grayish than that form. . . ." Although he referred The Dalles skins at that time to *strigata,* it is unlikely that *strigata,* being confined as it is to the humid coast section west of the Cascades, penetrates very far eastward along the Columbia River. These smaller, less grayish individuals of which Oberholser speaks fall into the same category as the rest of the examples from eastern Washington and Oregon near the Columbia River. They may be a result of intergradation between *merrilli* and *lamprochroma;* or perhaps they represent another center of differentiation in the Columbia River region of eastern Washington and Oregon. It is not improbable that these brownish specimens are intergrades and at the same time local differentiates. The least likely of all possibilities is that they are directly related to *strigata.*

That birds from the extreme northern part of the range of *merrilli* show no approach to *arcticola* has been stated in the previous subspecies account. The series from Riske Creek Post Office, British Columbia, are from a lowland locality. Taken late in July, they are in worn plumage, but their outstanding character is their blackish appearance. Also, the throats are uniformly deep yellow. In these characters as well as in their measurements they are almost

exactly like breeding examples of *merrilli* from the Madeline Plains of Lassen County, California. They differ only in their slightly duller napes. The single juvenile from Riske Creek is like juvenal examples of *merrilli* from more southern localities. Specimens from Okanagan Landing, British Columbia, although dark like *merrilli* and of the same size, have a more ashy (less ruddy) cast to the nape.

Brooks and Swarth (1925:77), in their account of *merrilli*, state that horned larks from the Chilcotin Plateau, British Columbia, although recorded as *merrilli* (Brooks, 1903:282), may represent an undescribed race. It now appears that these birds, despite the northerliness of their locality, are almost typical of *merrilli*.

The yellow wash on the underparts, so conspicuous in the races *strigata* and *sierrae*, crops up in certain examples of *merrilli* but only in a small percentage. Of all the specimens of the race that I have examined, only five have yellow on the underparts, and all of these are fall or winter examples. Of these, the most conspicuous are three from Cecil, Morrow County, Oregon. In their wing length and blackish back they are like *merrilli*, but they have the yellow below and an unusually deep tone of color on the flanks and the bend of the wing. It is possible that these last two characters show relationship to *strigata*.

Otocoris alpestris lamprochroma Oberholser

Warner Valley Horned Lark

[*Otocorys alpestris*] *arenicola* Henshaw (1884:259), part
Otocoris alpestris praticola, Dwight (1890:146), part
Otocoris alpestris merrilli, Bendire (1895:346), part; Oberholser (1902:833), part; Ridgway (1907:315), part; Taylor (1912:376); Grinnell and Storer (1924:374), part; Mailliard (1927:308); Grinnell, Dixon, and Linsdale (1930:285), part
Otocoris alpestris lamprochroma Oberholser (1932:4), original description; Linsdale (1936:80)

Type.—Adult male, no. 15005, Cleveland Mus. Nat. Hist.; Spanish Lake, east base of Hart Mountain, northern end of Warner Valley, twenty miles northeast of Adel, Lake County, Oregon; June 12, 1930; collected by Alex Walker; original number 2557.

Diagnosis.—Of a gray-brown appearance in fresh plumage, darker and browner than the ashy gray of *utahensis*, but lighter in color than that race when wear and fading have progressed; lighter, appearing more bleached than *merrilli* at all times of year, with more ruddy on nape and less break between nape and back color; larger and duller than *ammophila*; grayer than *sierrae* and lacking the ruddy brown and yellow underparts. The dorsal coloring of this race in fresh plumage most closely approaches Hair Brown. The nape in fresh plumage varies from Light Cinnamon to Drab, being Wood Brown or Avellaneous in worn state.

Measurements (in millimeters).—Breeding males (70 specimens): wing, 101.7 (107.9–96.8); tail, 68.2 (73.6–62.0); bill from nostril, 9.5 (10.3–8.3); tarsus, 20.8 (22.1–19.1); middle toe without claw, 10.4 (11.8–9.0).

Breeding females (42 specimens): wing, 95.0 (100.1–91.0); tail, 60.3 (64.5–56.0); bill from nostril, 8.9 (10.3–8.2); tarsus, 20.4 (22.0–18.1); middle toe without claw, 10.2 (11.3–8.8).

Distribution.—Breeds in the western part of the Great Basin, including southeastern Oregon, extreme southwestern Idaho, extreme northeastern California in the Honey Lake region, Lassen County, and east of the Warner Mountains; also in central eastern California in the Mono Lake area, and in western Nevada west of the 118th meridian. In winter, ex-
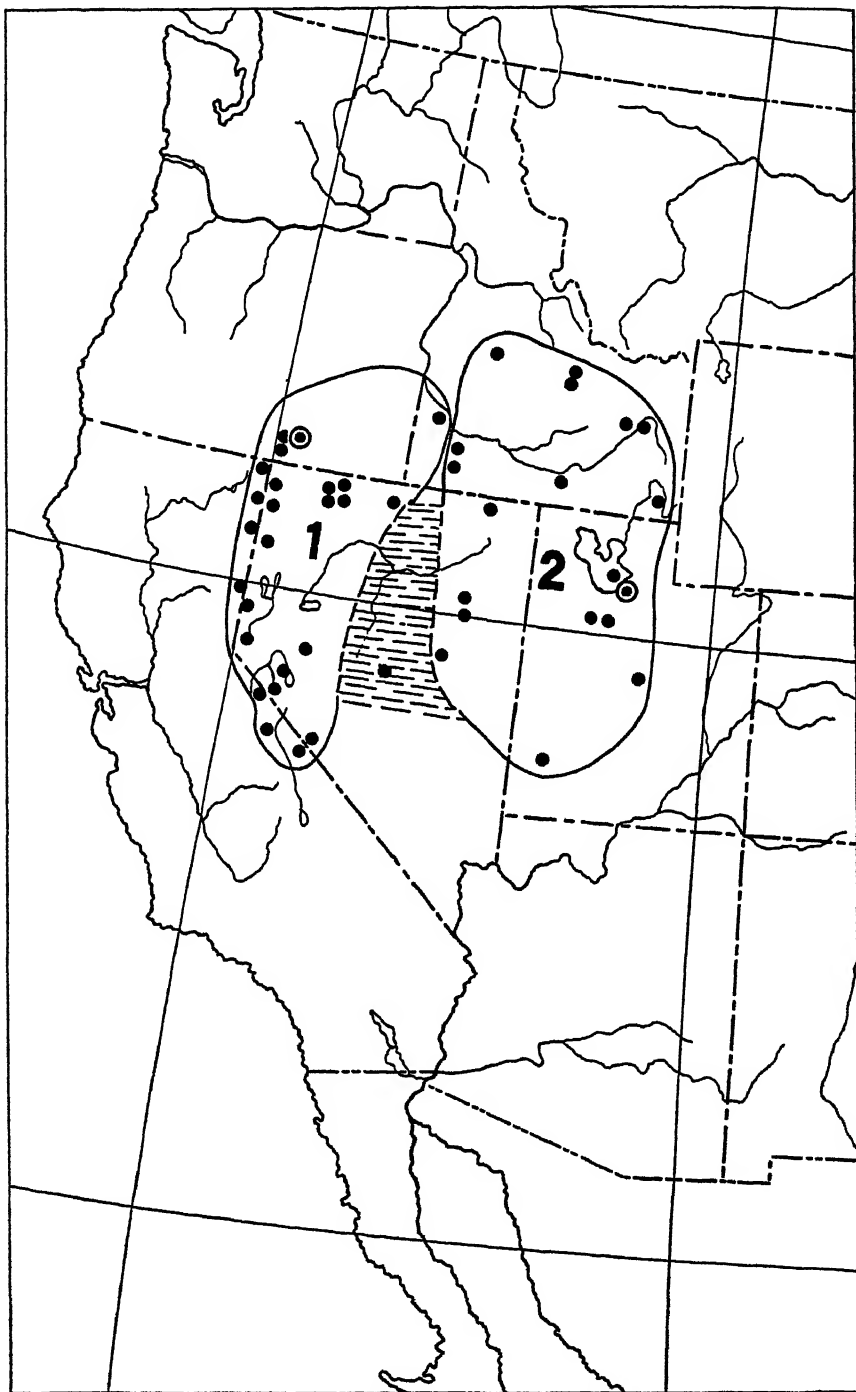
Fig. 3. Breeding ranges of the two races of horned larks in the Great Basin: 1, *O. a. lamprochroma*; 2, *O. a. utahensis*. Plain dots indicate breeding localities from which specimens have been examined; encircled dots show type localities; zone of intergradation indicated by shading.

amples are to be found within the breeding range, but many also occur in the Sacramento and San Joaquin valleys of California and in southeastern California.

Specimens examined.—The number of specimens of this race totaled 280. Of these, 79 were breeding males, 52 breeding females, 81 autumn and winter males, 38 autumn and winter females, and 30 juveniles. The localities whence these examples came are listed below, together with the number of specimens from each place. All specimens are in the Museum of Vertebrate Zoölogy unless otherwise indicated. Breeding localities are marked with an asterisk.

OREGON.—Harney County: Saddlebutte, 1 (Jewett coll.). Lake County: Spanish Lake, east base Hart Mt., 1 (Jewett coll.) ; 2 mi. N Plush, 34; Adel*, 2 (Dickey coll.).

IDAHO.—Owyhee County: 5 mi. SE Murphy*, 2. Cassia County: 10 mi. W Burley, 2. Minidoka County: 12 mi. W Rupert, 1.

NEVADA.—Humboldt County: Martin Creek Ranger Station*, 1; 5 mi. N Paradise Valley*, 1; Quinn River Crossing*, 27; Hot Spring, Thousand Creek*, 1; Leonard Creek, 1; Alder Creek*, 1; Big Creek Ranch*, 1; Virgin Valley*, 2; 6 mi. N Duffer Peak*, 5. Washoe County: 4 mi. S Diessner, 5800 ft.*, 1; 13 mi. S Vya, 5800 ft.*, 2; 17½ mi. W Deephole, 4750 ft.*, 2; 17 mi. NW Reno*, 1; 6 mi. NW Reno, 15. Ormsby County: Carson Valley*, 3 (Stanford Univ. coll.). Churchill County: 7 mi. N Stillwater*, 1; 10 mi. S Fallon, 1. Lyon County: 27 mi. S Fallon, 1. Mineral County: East Walker River, 5050 ft., 2 mi. NW Morgan's Ranch*, 2; 8 mi. S Schurz*, 1; Lapon Canyon, 8900 ft., Mount Grant*, 2; southwest slope of Mount Grant, 9400 ft.*, 2. Esmeralda County: 18 mi. W Tonopah, 1; Arlemont, 4900 ft., Fish Lake Valley*, 7. White Pine County: 4 mi. E Ruby Lake, 1 (Ellis coll.).

CALIFORNIA.—Modoc County: Cowhead Lake, 9; Eagleville*, 10 (Calif. Acad. Sci.); 3 to 5 mi. E Eagleville*, 4 (Calif. Acad. Sci.); 7 mi. E Cedarville, 1 (Calif. Acad. Sci.). Lassen County: 6 mi. N Observation Peak*, 6; 5 mi. N Fredonyer Peak, 2; 3 mi. N Standish, Honey Lake Valley, 1 (McLean coll.) ; Bull Flat, 5 mi. NE Hot Springs Mountain, 1 (McLean coll.); ½ mi. SE Edgemont, Honey Lake Valley, 1 (McLean coll.); Mud Flat, 6 mi. N Wendel, 1 (McLean coll.); Horse Lake, 1 (Calif. Acad. Sci.); Red Rock, 25 mi. NE Termo*, 1 (Stanford Univ. coll.). Nevada County: Truckee, 13. Placer County: Ward Creek, 3½ mi. W Lake Tahoe, 2 (Moffitt coll.). Mono County: Bodie*, 6 (Calif. Acad. Sci.) ; Sand Flat, Mono Lake*, 3; Farrington's Ranch, Mono Lake*, 2; Parker Creek*, 1; Convict Creek*, 9; Casa Diablo Hot Springs*, 5 (Dickey coll.) ; Mammoth*, 9 (Dickey coll.) ; Owens River, 6800 ft., 4 mi. E Whitmore Tub, Long Valley*, 2; Benton Station*, 1 (Santa Barbara Museum) ; Big Prospector Meadow*, 10,500 ft., White Mountains, 28; Sheep Mountain, White Mountains*, 1; McAfee Meadow, White Mountains*, 4; south base White Mountain Peak*, 1. Inyo County: Olancha, 1. Imperial County: Imperial Valley, 1 (A. H. Miller coll.). Los Angeles County: Long Beach, 1 (Dickey coll.). Kings County: Hanford, 4; 15 mi. S Corcoran, 2. Mariposa County: Dudley, 1 (McLean coll.) ; 6 mi. E Coulterville, 2800 ft., 1; Ten Lakes, Yosemite National Park, 1. Merced County: Planada, 2. Sacramento County: Sacramento, 7 (Dickey coll.). Butte County: 7 mi. SE Chico, 1 (McLean coll.) ; 7 mi. SW Richvale, 1 (McLean coll.). Tehama County: 8 mi. S Corning, 5.

Habitat notes.—Horned larks of this race occupy arid desert country that is only sparsely covered with vegetation, chiefly greasewood (*Sarcobatus vermiculatus*), sagebrush (*Artemisia tridentata*), and rabbitbrush (*Chrysothamnus* sp.). The type locality exemplifies this sort of country. Much of the terrain within the range is flat and once formed the floors of lakes now dried up, such as those that formerly existed in the Harney-Malheur region of south-central Oregon, the Warner Valley of southeastern Oregon, the Surprise Valley of northeastern California, and the Black Rock, Snake Creek, and Humboldt-Carson sinks of Nevada. The playa lakes that at times cover these areas are ephemeral; they come and go with climatic fluctuations. At the present time, almost all of them are dry. The barren, creamy-yellow plains

remaining are sparsely covered with vegetation and are occupied by horned larks. In the range of *lamprochroma* we also find level-floored valleys between barren and rocky mountain ranges that run for the most part northeast and southwest. Horned larks occur in these valleys and up on the alluvial lower slopes of the mountains. These mountain ranges represent the remnants of upturned blocks of the earth's crust and do not form continuous barriers; rather, they form individual islands in the surrounding plain and so affect only slightly the distribution of these birds. As contrasted with conditions in the ranges of *sierrae, merrilli,* and *strigata,* nowhere within the range of *lamprochroma* does one find horned larks in areas surrounded by coniferous forests.

Nomenclatural history.—The distinctive characters of horned larks from the range now ascribed to *lamprochroma* were first noted by Dwight, who stated in his introductory paragraphs (1890:139) that "Among the surprises developed by the material before me, is the existence of a form on the eastern slope of the Sierra Nevada Mountains, referable directly to *praticola.*" Thus the eastern form *praticola* was given by this author a divided range, with another race interposed between the two sections. Further remarks on this divided range were made by Oberholser (1902:835) as follows: "Summer specimens from the vicinity of Carson and Pyramid Lake, Nevada, are noticeably paler than typical *merrilli,* thus being exceedingly similar to *praticola,* to which form Dr. Dwight has referred the birds from Carson. The males are practically indistinguishable, either in size or color, from *praticola,* but the females average somewhat paler. This difference is so slight, however, that were the birds from an area contiguous to the region inhabited by *praticola,* they would unhesitatingly be considered as belonging to that race; but geographically situated as they are, practically between the ranges of *leucolaema* and *merrilli,* it seems much more rational to consider them intermediates between these forms, and as such to refer them to the one which they seem more closely to resemble. The only alternatives are to recognize them by name, which does not seem advisable in view of their practical identity with *praticola,* or to call them *praticola,* with explanation of the divided range thus assigned to the latter."

Mailliard (1927:308) encountered horned larks of this race in Surprise Valley in the vicinity of Eagleville, Modoc County, California. He made the comment that "the two adults taken in spring are appreciably paler than most of our specimens of similar date from Siskiyou County (California)." Finally, in recent years with the receipt of new material chiefly from the Warner Valley in southeastern Oregon, Oberholser gave a new name to the horned larks of the western part of the Great Basin. But he still considered the ones from Carson Valley not typical of *lamprochroma,* for he wrote (1932:5): "Specimens from the vicinity of Carson, and of Pyramid Lake, Nevada, which have sometimes been referred to the eastern *Otocoris alpestris praticola,* are really nearer this new race [*lamprochroma*], although, of course, somewhat intermediate between it and the geographically adjoining forms, *Otocoris alpestris leucolaema* and *Otocoris alpestris sierrae.*"

In order to investigate this newly proposed race and to clear up the confusion relating to horned larks in western Nevada, I made a visit to the Warner Valley, the type locality of *lamprochroma*, late in August, 1934, at which time I judged the horned larks would have nearly completed their molt and yet would be in the vicinity of their breeding grounds. A series of thirty-four specimens was collected from an old lake bed about two miles north of Plush. Both sexes are represented in the series; some are adults, others are first-year birds. On this same trip, other material representative of the race was collected at more southern points in California and Nevada. Comparative material was also obtained from the ranges of *merrilli* and *sierrae*. Chiefly upon the basis of these specimens, I am now able to state that the race *lamprochroma* is readily distinguishable in typical form and is worthy of recognition. This fresh fall material shows little, if any, close similarity to eastern birds of the race *praticola*. Although worn birds tend to look more like examples of *praticola*, at the same time it is to be remembered that certain diagnostic characters are lost with wear and fading. Examples from Carson Valley are fairly typical of *lamprochroma*, being the same in appearance as the rest of the specimens of the race from southeastern Oregon and Nevada. They are not intermediate between *praticola* and the geographically adjoining forms, *leucolaema* and *sierrae*, as Oberholser once stated.

Distribution and variation.—As nearly as I can ascertain from the material at hand, there is a fair degree of uniformity in general appearance among examples of this race from all parts of the range except where intergradation takes place with neighboring races. In nearly every example where intergradation has been detected, the areas of intergradation with contiguous races are large. The most typical specimens of the race seem to occur in that part of its range extending from the Warner Valley in southeastern Oregon south to Mono Lake, California. Elsewhere, examples show approaches in certain features toward those in other neighboring centers of differentiation.

Material representative of the race in the southern part of its range has been fairly abundant but consists chiefly of breeding birds and so is not comparable with fresh-plumaged birds from farther north. Breeding birds from Bodie, Mono County, California, are like those from the Pine Forest Mountains in Humboldt County, Nevada, and from the Warner Valley, Oregon. They are also similar to those from Convict Creek and other localities southwest of Mono Lake. A single male taken at Benton Station, Mono County, on May 30, 1936, is without doubt referable to *lamprochroma* since it is exactly like those examples just mentioned from Bodie and elsewhere. But south of this locality, intergradation probably occurs with *ammophila*. It further appears that the intergradational area is confined to lower altitudes in the upper Owens Valley and that specimens typical of *lamprochroma* are found at the higher elevations of the Mono Lake area.

Several breeding specimens from Arlemont, Esmeralda County, Nevada, a locality east of Benton Station and situated in the upper end of Fish Lake Valley, are referable to *lamprochroma*, but they are not typical; they show an approach to *ammophila*. From Oasis, Mono County, California, south of

Arlemont and in the same valley, several examples in fresh plumage were taken from August 25 to 29, 1922, at a time when they were just completing their autumnal molt. Thus it can be reasonably assumed that these were on or near their breeding grounds when collected. These specimens are intermediate in their characters between *lamprochroma* and *ammophila*. It seems, then, that *lamprochroma* blends southward into *ammophila* in Fish Lake Valley and that the trend commences at least as far north as the neighborhood of Arlemont.

In between these two areas of intergradation, from Benton south and from Arlemont south, we have an interesting phenomenon: a strip occupied by more typical *lamprochroma* seemingly extends southward at high altitudes in the White Mountains in Mono and Inyo counties, California. In the collection of the Museum of Vertebrate Zoölogy is a series of thirty-four horned larks from the White Mountains, taken in late July, 1917, chiefly at Big Prospector Meadows, 10,500 feet, though some were obtained at McAfee Meadow, 12,000 feet. The highest altitude at which any single individual was taken was 13,000 feet, at the south base of White Mountain Peak. In the field notes of the collectors of these specimens it is stated that the birds were shot from small flocks at the termination of the nesting season. Bobtailed juveniles and adults were abundant in the short-grass meadows and among areas of dwarf sagebrush on the edges of the meadows. In one notebook I find the comment that their call notes and actions were the same as those of the birds in the lowland areas.

The adults of this series are badly worn. However, they differ little from comparable specimens from Humboldt County, Nevada. More indicative of relationships is the fact that the juveniles are just like those from Humboldt County, and also like those from Convict Creek in Mono County, California. One immature female in the Dickey collection, no. J-1497, taken August 3, 1921, at Big Prospector Meadows, still retains some juvenal feathers but is almost completely molted. The centers of the back feathers are dark with the edges lighter, producing an appearance much like that of fall examples from north of Reno. Furthermore, the measurements of the White Mountains series average close to those of the large series from Quinn River Crossing, Humboldt County, Nevada; they are distinctly larger than *ammophila*. The evidence indicates that these White Mountains examples do not approach any other race and are fairly typical of *lamprochroma*.

Since these White Mountains specimens come from an isolated section, one might have expected local differences, but I have been unable to detect any. The high altitude does not seem to have been a limiting factor in local distribution in this instance. The White Mountains examples are just like other members of the same race from farther north in Nevada, differing appreciably from the intergrades with *ammophila* several thousands of feet below. Apparently only the lowland population has become intergradational through contact with the neighboring race *ammophila*. Interbreeding would not be so likely with the birds in the isolated boreal meadows, hence presumably the population there has remained more representative of *lamprochroma*.

Details of the intergradation between *lamprochroma* and *utahensis* are dis-

cussed under the latter name. However, it may be remarked here that the blending probably takes place over a wide area in central and eastern Nevada. In making distribution maps and delimiting the ranges of subspecies, one frequently faces a difficult problem, as in this illustration, in deciding where to draw the line separating the two races. As often as not, the decision must be made arbitrarily. Wherever it has been possible to·do so, I have taken into account the physiographic features. This is particularly true in the present instance, for the following reasons. In Nevada, there is an eastern high plateau area averaging about 6000 feet in elevation. In the western part of the state there is a contrastingly lower country that averages perhaps 4000 feet in elevation. It is in this lower portion that we find prominent "sinks"—the Humboldt-Carson Sink and others. The transition from this low area to the higher plateau occurs east of Fallon, Lovelock, and Winnemucca. *Lamprochroma* is characteristic of the lower westernmost part of the state. In the higher eastern section we find differences indicating intergradation. It seems logical, in the light of the gradual blending of characters, to separate the two races in the transitional area along a line where the rise in elevation commences. This line corresponds closely with the ancient shore line of Lake Lahontan. In fact, it is striking that in western Nevada the greatest part of the range of *lamprochroma* does occupy the bed of this Pleistocene lake.

The large series of *lamprochroma* at hand from the Pine Forest Mountains in Humboldt County, Nevada, affords some idea of the range of individual variation in the race. Although there is, in general, a uniformity of appearance among the specimens, two instances of extreme variation attract attention. A male taken June 9, 1909, in Virgin Valley, evidently a breeding bird, represents the very dark extreme and resembles examples of *merrilli* from far to the west. This coloration seems best attributed to extreme individual variation, but there is the possibility that this specimen is really an example of *merrilli* that was far out of range, perhaps having joined a flock of *lamprochroma* during the winter and then migrated with them back to their breeding grounds. Miller (1935:468) has reported a pair of juncos of mixed characters apparently breeding in these Pine Forest Mountains.

The other unusual specimen stands out as being extremely brown in its entire plumage. This juvenal female (no. 8605, Mus. Vert. Zoöl.), with molt nearly complete, resembles the eastern race *praticola*. It may be that the intensity of brown is an age or sex difference, but this is highly improbable in the light of the comparisons I have made and discussed in the sections on variation. A juvenile from Quinn River Crossing in the Pine Forest Mountains is also very brown; it thus seems that we have here simply examples of extreme individual variation. It is possibly such very brown juveniles that develop into the very brown adults.

In the region north of Honey Lake in Lassen County, California, *lamprochroma* intergrades with *merrilli*. This area of intergradation occurs, significantly, at the southern end of the Warner Mountains where this barrier dividing the two races ceases to exist. The blending of the two races in this region is progressive, but the intergradational area is not of great extent.

Evidence for intergradation with *merrilli,* based on breeding birds, is presented in the systematic account of that race. Two specimens of *lamprochroma* with a suffusion of yellow below, as in *sierrae,* indicate possible contact with that form. Both are winter birds. One was taken January 24, 1935, three miles north of Standish, Honey Lake Valley, Lassen County; the other, December 31, 1934, seven miles southwest of Richvale, Butte County, California.

In the northern part of the range of *lamprochroma,* there are indications that intergradation with *merrilli* again occurs, but this time over a wide area. Oberholser (1932:5) has stated that the range of *lamprochroma* extends north to the mouth of the Deschutes River but that specimens from there tend to approach *merrilli.* That the range of *lamprochroma* does not extend as far to the north and west as the mouth of the Deschutes River is indicated by the breeding example of *merrilli* from near Shaniko, Wasco County, Oregon, previously discussed. This locality is south and a little east of the mouth of the Deschutes River. However, a few representatives from southeastern Washington and northeastern Oregon, both breeding and nonbreeding birds, show an increased amount of ruddy on the nape, and their backs are browner. They are also less grayish than typical examples of *lamprochroma.* The color of the backs of worn specimens is such that they seem to be intermediate in color tone between the more blackish *merrilli* and the grayer *lamprochroma.* The increased ruddy tone is apparently a local peculiarity.

At the present time, with the scanty material at hand, the best explanation seems to be that there is a large area, the precise extent of which is unknown, where *merrilli* and *lamprochroma* blend. Also in this area there seems to be another of the numerous lesser centers of differentiation now so frequently noticed. On the basis of the material at hand, the birds in this area are not sufficiently distinct to justify a new subspecific name. Until more material is available, I prefer to refer them to *lamprochroma,* at the same time recognizing the signs of local differentiation and the intermediate nature of the representatives. Examples in this category are as follows:

WASHINGTON. Whitman County: Pullman*, 3 (Stanford coll.). Grant County: Quincy*, 2 (Dickey coll.). Adams County: Othello, 4 (Dickey coll.). Benton County: Kiona, 9 (Dickey coll.). Asotin County: Silcott*, 1 (Jewett coll.).

OREGON. Umatilla County: Hermiston*, 1 (Jewett coll.). Wallowa County: Zumwalt*, 1 (Jewett coll.). Union County: La Grande*, 1 (Santa Barbara Mus.). Baker County: 11 mi. E Unity, 4 (Dickey coll.).

IDAHO. Canyon County: Nampa, 2 (Dickey coll.).

Oberholser (1902:835) states that "Breeding examples from Steens Mountains in southern Oregon have the lighter portions of the upper surface considerably suffused with reddish, and the back is more brownish black than ordinary birds, thus strongly resembling *strigata* in color, though sufficiently different in size." He further states (*loc. cit.*) that "Birds from Fort Harney, Oregon, are quite similar to those from the Steens Mountains." From these comments I would judge that the birds to which he had reference were like the ones from Quincy, Grant County, Washington, and others which I have already discussed.

The race *lamprochroma* offers one of the best examples encountered of a certain situation prevalent in the variation in horned larks, that is, the connection of a racial center of differentiation with all the surrounding ones by progressive intergradation. On the north *lamprochroma* passes into *merrilli;* on the south it passes into *ammophila.* In this broad area certain characters considered diagnostic of the race are most highly developed; most of the birds occurring here we call typical examples of the race, but variations are numerous. To the east, *lamprochroma* intergrades with *utahensis* and so becomes a part of an east-west trend across the Great Basin. Physical barriers separate it for the most part from *sierrae.*

Winter distribution.—Several winter-taken birds indicate that the San Joaquin Valley is one place of winter residence for birds of this race. Several fall and winter records in the Sierra Nevada suggest that members of the race may migrate over the divide of these mountains on their way to the San Joaquin Valley. This crossing may occur, it seems, in the Yosemite region. A male (no. 25935, Mus. Vert. Zoöl.) was taken at Ten Lakes, Yosemite Park, on October 11, 1915. Another male (no. 26361, Mus. Vert. Zoöl.) is at hand from Smith Creek, 6 miles east of Coulterville, Mariposa County, taken January 20, 1916. Winter examples are numerous from Hanford and from 15 miles south of Corcoran, Kings County, and from Planada, Merced County. A pair taken south of Corcoran on February 22, 1932, had gonads slightly enlarged. Those from Hanford were taken February 21, 1929, and were extremely fat.

In another year and at an earlier date than those at which the Kings County examples were taken, members of this race on the east side of the Sierra Nevada were already moving north. Between February 15 and 18, 1935, Mr. L. Morgan Boyers shot twelve horned larks at snow-free patches of ground along the railroad tracks at Truckee, Nevada County, California. These were sent to me, and although some are covered with soot, they are without doubt of the race *lamprochroma.* Two or three of the lot have the increased amount of ruddy and the brown dorsal coloring which we have noted as characteristic of birds from northeastern Oregon along the Columbia River.

There can be no question that these were migrating birds, for it is the race *sierrae* that breeds in the Truckee region. No horned larks were observed prior to the arrival of the birds that were obtained. Also, these birds were taken in a heavily timbered country on the east side of the crest of the mountains. This circumstance, together with the occurrence of members of the race in the autumn at Lake Tahoe and in the Yosemite region, leads to the suggestion that there is some sort of fly line along the mountains on the east side of their crest. Presumably, the autumnal crossing of the mountains is made in the Yosemite region, whence the line of flight continues westward down into the lower San Joaquin Valley. But of course more field work has been done in the Yosemite area and more bird students are stationed there than in other parts of the Sierra Nevada.

That *lamprochroma* winters in part in the Sacramento Valley of California is indicated by specimens taken seven miles southwest of Richvale, Butte County, seven miles southeast of Chico, Butte County, and eight miles south

of Corning, Tehama County. On the other hand, some members of the race, presumably those from the southern part of the range, must move more directly south into southeastern California and probably Arizona. Winter examples are present from Olancha, Inyo County, the Imperial Valley, and Long Beach, Los Angeles County, California. Oberholser has recently identified two specimens taken in winter at the Wupatki National Monument, Arizona, as of this race (see Hargrave, 1936:121). I have examined these specimens, however, and do not agree with this identification (see discussion under *occidentalis*). The record for Texas (Stevenson, 1937:44) may also be doubtful.

Some individuals of *lamprochroma* remain within the breeding range throughout the winter. There are many winter examples in the McLean collection from the Honey Lake Valley region. Throughout the winter of 1933–34 he observed a flock of 15,000 horned larks in Honey Lake Valley (McLean, 1936:17). This particular winter was a severe one, and the birds were frequenting areas of Russian thistle. In contrast, the winter of 1935–36 was relatively mild in the Honey Lake Valley and no such huge flocks were observed. Rather, the larks remained in flocks of only a few hundred individuals. The last big snowstorm in 1936 occurred during the first week in March. As soon as the weather cleared up, according to McLean, the horned larks seemed suddenly to move out of the valley in small groups, chiefly to the north and east. By March 6, pairs were seen scattered around Mud Flat and other open areas to the north. This date fits in fairly well with the dates of the Truckee migrants of the previous year and certain nesting data on horned larks along the Columbia River. Decker (1926:41) took nests and eggs of horned larks on March 15 and found the eggs heavily incubated. Young were out of nests by the last of March. McBee (1931:43) found a nest with young four or five days old on March 17, 1927. We might infer from these data that the majority of horned larks of this race have returned to their nesting grounds by about the first week in March and that in mild winters they do not tend to bunch up as much as in severe winters. Also, the return migration is probably earlier in years of mild winter and early spring.

Otocoris alpestris utahensis Behle

Great Salt Lake Horned Lark

Eremophila alpestris, Henshaw (1874*a*:6); Henshaw (1874*b*:45); Henshaw (1875: 309), part

[*Eremophila alpestris*] v. *chrysolaema*, Ridgway (1877:500), part

[*Otocorys alpestris*] *arenicola* Henshaw (1884:259), part

Otocoris alpestris arenicola, Dwight (1890:146), part

Otocoris alpestris leucolaema, Oberholser (1902:820), part; Ridgway (1907:309), part; Grinnell (1934:67); Linsdale (1936:79)

Otocoris alpestris utahensis Behle (1938:89), original description

Type.—Adult male, no. 66312, Mus. Vert. Zoöl.; 10 mi. W Salt Lake Airport, Salt Lake County, Utah; September 11, 1934; collected by D. M. Behle.

Diagnosis.—Most nearly like *lamprochroma* but slightly larger, darker in worn plumage but more grayish, less brownish in fresh fall plumage; smaller than *enthymia*, with more yellow on throat and eyestripe; smaller, more grayish than *leucolaema*, particularly in

unworn plumage lacking sandy brown dorsal color of latter; juveniles paler, less brown than in *leucolaema;* of about same size as *occidentalis* but lacking dusky brown, being chalky gray instead; slightly larger than *leucansiptila*, with less of bleached pink appearance. Color of nape in fresh fall plumage, Light Drab or Drab-Gray, blending with color of back, which is nearer Drab; in worn plumage, nape varies in color from Cinnamon Drab or Light Cinnamon Drab to Fawn, while the back seems closest to Natal Brown.

Measurements (in millimeters).—Breeding males (38 specimens): wing, 103.9 (107.5–100.4); tail, 70.4 (74.2–66.0); bill from nostril, 9.5 (10.5–8.1); tarsus, 21.2 (23.0–20.0); middle toe without claw, 10.8 (12.2–9.5).

Breeding females (12 specimens): wing, 96.6 (99.5–95.0); tail, 62.7 (66.0–60.0); bill from nostril, 9.1 (9.8–8.5); tarsus, 20.5 (21.2–20.2); middle toe without claw, 10.5 (11.8–9.2).

Distribution.—Breeds in the eastern half of the Great Basin, that is, in Elko and White Pine counties in eastern Nevada, in Utah west of the Wasatch Mountains, and from south-central Idaho at least, south to west-central Utah and east-central Nevada. In winter, members of the race occur in southeastern California and probably in Arizona.

Specimens examined.—The number of examples of this race that I have examined totals 202. Of these, 48 were breeding males, 21 breeding females, 68 autumn and winter males, 57 autumn and winter females, and 8 juveniles. The localities represented by these specimens are listed below together with the number of specimens from each place and their place of deposit. Unless otherwise indicated, specimens are in the Museum of Vertebrate Zoölogy. Breeding localities are marked with an asterisk.

IDAHO.—Custer County: Pahsimeroi Valley, 6–10 mi. S Goldburg*, 5; head of Pahsimeroi River*, 2. Valley County: Bear Valley, 5 mi. E Elk Creek Ranger Station*, 3. Bonneville County: 17 mi. W Idaho Falls*, 3. Lake County: Bloomington*, 2 (Univ. Utah coll.). Cassia County: 3½ mi. S Declo*, 2. Owyhee County: 10 mi. N Riddle*, 1; 30–34 mi. N Riddle*, 2.

UTAH.—(All specimens listed from Utah in University of Utah collection with four exceptions as noted). Davis County: Antelope Island*, 2; West Bountiful, 2. Salt Lake County: West Salt Lake City*, 5; 5 mi. W Salt Lake Airport*, 9 (Mus. Vert. Zoöl.); 10–15 mi. W Salt Lake Airport, 14 (Mus. Vert. Zoöl.). Tooele County: Skull Valley*, 1; Rush Lake, 3; Rush Valley*, 2; Stockton, 1. Sanpete County: 5 mi. E Great Basin Experiment Station, Wasatch Mountains*, 2 (Mus. Vert. Zoöl.). Iron County: Lund*, 2 (Dickey coll.). Washington County: St. George 1.

NEVADA.—Elko County: 3 mi. N Jarbidge*, 7 (Ellis coll.); 18 mi. NW to 17 mi. SW of Currie, 9; North end Ruby Lake*, 2 (Ellis coll.); Hobson*, 1 (Ellis coll.). White Pine County: 7 mi. SE Hobson P. O.*, 4 (Ellis coll.); Lincoln Highway, 15 mi. SE Eureka, 1; Spring Valley, 17 mi. N Geyser, 16. Lincoln County: 20 mi. W Caliente, 1; 1 mi. S Hiko, 4000 feet, 5. Pershing County: Mill City, 1. Churchill County: 10 mi. S Fallon, 18. Mineral County: Near Schurz, 10. Esmeralda County: 18 mi. W Tonopah, 7. Nye County: 14 mi. NW Beatty, 1; 5 mi. SE Millett P. O.*, 19; South Twin River*, 6000 feet, 1.

CALIFORNIA.—Kern County: Southwest part Walker Basin, 3350 feet, 17; Rankin Ranch, Walker Basin, 3300 feet, 2. Inyo County: Surveyor's Well, –60 feet, Death Valley, 2; 4 mi. SSE Junction Ranch, 5700 feet, Argus Mountains, 13.

Habitat notes.—In the broad features of habitat occupied, this race does not seem to differ from *lamprochroma*. I have found *utahensis* breeding on the "salt flats" west of Salt Lake City where the country is flat and level and sparsely covered with greasewood (*Sarcobatus vermiculatus*), hop-sage (*Graya spinosa*), and sage (*Artemisia tridentata*). On Antelope Island, Great Salt Lake, I have seen them on more rolling terrain, chiefly open grassland. In Rush Valley, Tooele County, Utah, they are numerous around farms in open fields. Miller (1934:161) found horned larks which seem to be closest to this race in open places as high as 10,000 feet north of Fish Lake, Sevier

County, Utah, in the Wasatch Mountains. A few were seen by him in the drier parts of the meadow. They were abundant on the divide east of Ephraim on barren ground and also along small streams running from the snow banks in early July. In winter one finds them on snow-free, semirocky slopes or along roadsides where Russian thistle is abundant.

Distribution and variation.—The race *leucolaema* as understood at the time of Oberholser's revision possessed a range of vast extent. The many local variations within this range were considered by Oberholser to be "independent of subspecific relationship or intergradation." The accumulation of a great amount of new material from the area of one of these local variations has revealed constant differences in certain characters. These differences seem to be of sufficient intensity and uniformity to justify elevating to subspecific rank the population of the eastern part of the Great Basin.

In this connection it is interesting and important to note that two previous reviewers, each with scanty material at hand, commented on the fact that birds from localities within the range of *utahensis* as now defined were different from those of surrounding regions. Dwight (1890:146) stated that "birds from the desert region of Utah, near Great Salt Lake, are paler with a reddish cast of plumage similar to specimens from northern New Mexico, Arizona and Western Texas. . . ." Oberholser (1902:823) commented: "The birds examined from Antelope Island, Great Salt Lake, Utah, are conspicuously redder than those from the surrounding region, being thus curiously similar to *occidentalis,* though separated from this form by a wide area."

The material at hand representative of *utahensis* indicates that specimens from the immediate Great Salt Lake region are to be considered as the most typical of the race. Birds from that region average smallest for the race; they are the most ruddy on the nape; and in fresh plumage they are the grayest. Also, the nearly universal presence of deep yellow on the throat, eyestripe, and forehead is a conspicuous feature. In worn plumage, the backs of specimens are somewhat reddish, as has been noted. Even in fresh plumage a slight pinkish hue pervades the dorsum and mixes with the ashy gray.

There are at hand no examples of this race in fresh fall plumage from southern Idaho although several localities are represented by breeding birds. Breeding males from 3½ miles south of Declo, Cassia County, and 10 miles, 30 miles, and 34 miles, respectively, north of Riddle, Owyhee County, are practically the same in appearance as specimens from the alkaline flats west of Salt Lake City, Utah. The Idaho examples average a little larger in their measurements, however. A pair of worn birds from five miles east of Elk Creek Ranger Station in Bear Valley, Valley County, are perhaps referable to this race; a slightly deeper color on the nape together with the darkness of the back may indicate an approach to a more northerly or westerly form, probably *merrilli.*

However, breeding examples taken to the eastward in the Pahsimeroi Valley, Custer County, Idaho, are larger than Utah birds and lack yellow on the forehead and eyestripes. In this absence of yellow and in the increase in size they exhibit an approach to the birds of Montana and farther north, which have been variously considered as *enthymia* or *leucolaema.*

Although Merriam (1891:99) gives no localities from which horned larks were obtained during his biological survey of Idaho, he states that they were abundant throughout the sage plains and valleys. This evidently refers to those plains along the Snake River, where his itinerary took him. Immature and spotted young, he said, were very pale and hence widely different from eastern examples of *praticola*. In making this statement he touched on one of the most significant differences between *utahensis* and both *praticola* and *leucolaema*. The juveniles from the range of *utahensis* are decidedly paler than those from the range of *leucolaema,* as around Denver, whence I have had comparative material.

Little is known of the northern limits of the range of *utahensis*. It appears, however, that birds from the extreme southern part of Idaho south of the Snake River plains, that is, the Great Basin area of Idaho, are typical of the race, whereas individuals from the central and northern part of the state commence to show tendencies toward more northerly races.

The races *utahensis* and *lamprochroma* apparently come into close contact in southwestern Idaho and northeastern Nevada. Breeding horned larks from Murphy, Owyhee County, Idaho, are referable to *lamprochroma*. Yet specimens taken a short distance away, some 30 or 34 miles north of Riddle, Owyhee County, Idaho, are closest to *utahensis*. Examples from Martin Creek, in the Santa Rosa Mountains, Humboldt County, Nevada, are of the race *lamprochroma,* whereas breeding representatives from 3 miles north of Jarbidge, Elko County, Nevada, are closest to *utahensis*. These two races must be rather sharply separated between these points, for the above specimens are not plainly indicative of intergradation between the two races. Of the Jarbidge birds, the two juveniles are very pale. Two of the five males are dark like *utahensis,* but the other three are much browner and thus show a likeness to the brown breeding population of Oregon along the Columbia River. This last-named population may extend south past the Steens Mountains in extreme southeastern Oregon.

Examples from the Ruby Lake region in southern Elko County, Nevada, in comparable state of wear to the Jarbidge skins, are very pale. Similar to the Ruby Lake specimens is a series of breeding birds from five miles southwest of Millett Post Office, Nye County, Nevada. The examples from both Ruby Lake and Millett average larger than do Great Salt Lake specimens of *utahensis,* yet they are much paler than typical *utahensis* in worn plumage. Thus they resemble *lamprochroma*. This fact, together with the intermediacy in dorsal color characters of examples in fresh plumage from both places, suggests that *utahensis* and *lamprochroma* intergrade over a wide area in central Nevada.

Perhaps the excessive pallor of the skins from Ruby Lake indicates the beginning of an approach to *leucansiptila* to the south. Specimens taken in late September in Spring Valley, 17 miles north of Geyser, White Pine County, and near Hiko, Lincoln County, are paler than specimens from 10 miles west of Salt Lake City, which are in comparable plumage and were taken in mid-September. A pair of breeding birds from Penoyer Valley, 17 miles north of

Groom Baldy, Lincoln County, Nevada, are intermediates, and though they are closest perhaps to *utahensis,* the increased extent of the nape color down onto the shoulder region and back indicates a trend toward *leucansiptila.* We seem to have, then, in southwestern Utah and southeastern Nevada, another of those long gradual transitions from one race into another.

Although members of the race *utahensis* have a rufescent color, this is of a dull tone and quite unlike the brighter brown of *occidentalis.* No material is at hand to indicate any transition from *utahensis* into *occidentalis.* Quite to the contrary, there is some evidence that *leucolaema* intervenes between the two.

Utahensis seems confined during the breeding season to the eastern part of the Great Basin. In Utah, the Wasatch Mountain chain probably acts as the natural boundary on the eastern border of its range. Examples present from extreme eastern Utah are referable to the race *leucolaema,* but in the southeastern part there is some evidence of a slight local center of differentiation. A male from Valley City, Carbon County, Utah, taken April 4, 1928, one from Grand County between Green River and Moab, taken April 7, 1934, and one from 12 miles west of Mexican Hat, San Juan County, taken May 1, 1935, are all alike and are characterized by a dorsal coloration of bright tawny brown. Though they are comparable to *leucolaema* in size and in predominance of brown, still these examples appear brighter, and the browns are appreciably paler. Specimens in fall plumage from the same region taken in the vicinity of Wellington, Carbon County, are sandy brown, somewhat like *leucolaema,* but they also have a peculiar tint on the nape different from that in *leucolaema.* It most nearly matches the Russet-Vinaceous of Ridgway (1912). Perhaps these aberrant specimens from the San Juan section of Utah indicate an approach to *occidentalis.*

Only seven juveniles of the race *utahensis* are available; four of these are from the region west of Salt Lake City. They are fairly uniform in coloration. All are pale and whitish, hence decidedly different from the browner individuals of the neighboring races *leucolaema* and *lamprochroma.* It seems significant that the single juvenile from Millett, Nye County, Nevada, is as pale as any of the rest and so is distinguishable from representatives of *lamprochroma* from Arlemont, Esmeralda County, Nevada, and from the Pine Forest Mountain area in Humboldt County, Nevada. Thus, even though the adults from Millett are not typical of *utahensis,* the juvenile is. This strengthens the supposition that the birds from this locality are to be placed with the Great Salt Lake race.

In all probability, some examples of *utahensis* remain during the winter within the breeding range of the race, but in general there is a replacement of the local populations by flocks of horned larks from more northern breeding grounds. Members of *utahensis* move southwestward to the Carson-Humboldt Sink in Nevada and farther south into California. Typical specimens in unworn plumage are present from several localities in the Mohave Desert region. In this connection it is to be recalled that Grinnell (1934:67), in discussing the horned larks taken by him in Death Valley, states that "in color-tone, these

fresh fall birds are ashier than any other examples of *leucolaema* I have seen from California; they most nearly match fall birds from Colorado, whence in migration they may have come." At the time that Grinnell wrote this statement, most of the materials upon which the account of this race is based had not been obtained. The two specimens that Grinnell discusses are exactly like early fall birds taken west of Salt Lake City. There is no doubt in my mind that the Death Valley specimens came from the breeding range of *utahensis*.

In the fall of 1934 Grinnell also collected fresh-plumaged horned larks typical of this race in the Mohave Desert region, at Junction Ranch, Argus Mountains, Inyo County; at the Los Angeles Aqueduct, 3100 feet, 5 miles west of Mohave, Kern County, California; and 1½ miles west of Fairmont, Los Angeles County. The specimens from the last two localities were in flocks with the resident race *ammophila*. A large series of November birds from the southwest part of the Walker Basin, Kern County, are in somewhat worn plumage and hence not so conspicuously characteristic of this race. Yet they are to be referred here. They, too, were mixed with a great many examples of *ammophila*.

The series of winter-taken horned larks in the Dickey collection, taken December 3, 1919, and December 11, 1920, 10 miles south of Ontario, Riverside County, and reported by Dickey and van Rossem (1922:94) as belonging to the race *leucolaema*, still seem as a group to be referable to that race. Some are unquestionably *leucolaema*, while others resemble *utahensis*. A winter example of *leucolaema* is present in the McLean collection from Deep Springs Valley, Inyo County, California. Thus it appears that examples of both *utahensis* and *leucolaema* winter in California. The specimen from El Valle de la Trinidad, 2500 feet, and those specimens from the Alamo River, 20 miles southwest of Pilot Knob, Lower California, Mexico, also seem closest to *leucolaema*, just as Grinnell (1928:144) has recorded them.

Dickey and van Rossem (1924:110) have recorded several specimens taken in midwinter from southeastern California as *O. a. enthymia*. Since *enthymia* differs from *leucolaema* in its paler, more grayish colors above, and since the Great Salt Lake birds likewise differ from *leucolaema* in these respects, it seems not improbable that the specimens listed as *enthymia* came from the eastern part of the Great Basin. With this possibility in mind, the specimens so designated by these workers have been examined. They are indeed paler than examples of *leucolaema*. I do not believe that they came from the Great Basin, however, for they are lighter brown above than the more rufescent eastern Great Basin specimens. In wing length, dorsal coloration, and the white eyestripe the specimens in question agree most nearly with examples taken in winter and spring from eastern Montana and northern Colorado. As such, they answer the description of *enthymia* except that they have a little too much yellow on the throat, cheeks, and forehead to be called typical. These specimens in my opinion still stand as California records for the race *enthymia* and so contribute to our knowledge of the migrations of that form. This being so, we get in southeastern California in winter a great influx of migrant representatives of *leucolaema, utahensis, enthymia, lamprochroma,* and possibly

merrilli, as well as wanderers of the more sedentary races, *actia, ammophila,* and *leucansiptila*.

Perhaps the most puzzling fact in connection with the distribution of *utahensis* is the presence of two races of horned larks in the Great Basin, a desert area with much the same arid conditions prevailing throughout. The race *lamprochroma* has a breeding range that conforms roughly with the lake bed of the Pleistocene Lake Lahontan. Similarly, the range of *utahensis* corresponds roughly with the area once covered by Lake Bonneville which was contemporaneous with Lake Lahontan. Further discussion upon this point will be deferred until a later section (see pp. 305–306).

Otocoris alpestris sierrae Oberholser

Sierra Nevada Horned Lark

Otocoris alpestris rubea, Oberholser (1902:853), part
Otocoris alpestris merrilli Dwight (1890:153), part; Oberholser (1902:835), part;
  Ridgway (1907:315), part; Grinnell, Dixon, and Linsdale (1930:285), part
Otocoris alpestris sierrae Oberholser (1920:34), original description; Dawson (1923:
  840); Grinnell (1932:285)

Type.—Adult male, no. 203534, U. S. Nat. Mus.; head of Pine Creek, Lassen County, California; June 13, 1906; collected by A. S. Bunnell, original no. 267. The type locality is more exactly stated by Grinnell (1932:285) as "head of PINE CREEK [probably near present Bogard Ranger Station, some 25 miles east-northeast of Lassen Peak], Lassen County."

Diagnosis.—Resembles *strigata*, having yellow beneath as in that race, but is larger, more ruddy brown, and with less streaking on the breast; distinguished from *rubea* by larger size, deeper ruddier brown on the back and more yellow on the underparts; back more ruddy than the blackish brown of *merrilli*, and further distinguished from that race by the presence of yellow on the underparts; likewise differs from *lamprochroma* in possession of ruddy brown rather than light brown dorsal coloration and of yellow below. The dorsum in fresh plumage is near Prout Brown, but fades and wears to Mummy Brown; occiput and nape, Raw Umber; bend of wing, sides of neck, breast, flanks, and rump, Chestnut, turning to Army Brown in worn plumage; underparts in fall, Straw Yellow, fading and wearing often to whitish with traces of Barium Yellow.

Measurements (in millimeters).—Breeding males (23 specimens): wing, 98.6 (102.7–94.5); tail, 64.8 (70.0–60.6); bill from nostril, 9.3 (10.5–8.4); tarsus, 20.6 (21.6–19.3); middle toe without claw, 10.3 (11.4–9.1).

Breeding females (5 specimens): wing, 91.9 (93.8–90.6); tail, 59.1 (61.0–57.0); bill from nostril, 8.8 (9.1–8.4); tarsus, 20.3 (21.2–19.8); middle toe without claw, 10.2 (11.2–9.8).

Distribution.—Breeds in the northern part of the Sierra Nevada and southern part of the Cascade Mountains from Fall River Valley (Pittville), Shasta County, California, on the north to Truckee, Nevada County, at least, on the south. In winter, occurs in Honey Lake Valley, Lassen County, and in the Sacramento Valley.

Specimens examined.—Skins representative of this race total 59. Of these, 29 are breeding males, 7 are breeding females, 9 are autumn and winter males, 3 are autumn and winter females, and 11 are juveniles. These skins were taken at the following localities. Those marked with an asterisk represent stations from which breeding specimens were taken. The place of deposit of the skins is indicated. All localities are in California.

Lassen County: 2½ mi. S Pittville*, 1 (McLean coll.); Bogard Ranger Station*, 6 (McLean coll.), 1 (Mus. Vert. Zoöl.); 3 mi. E Bogard Ranger Station*, 3 (McLean coll.); Bridge Creek Meadows*, 1 (McLean coll.); 6 mi. W Eagle Lake*, 1 (McLean coll.); Champ's Flat on Pine Creek*, 2 (Mus. Vert. Zoöl.); Eagle Lake (south end)*, 1 (Mus. Vert. Zoöl.); Merrillville, 1 (Mus. Vert. Zoöl.). Plumas County: Last Chance Creek*, 6 (McLean coll.); Red Clover Valley, 1 (McLean coll.); Little Queen Valley*, 1 (McLean coll.); Beck-

with*, 1 (McLean coll.), 1 (Mus. Vert. Zoöl.), 15 (Dickey coll.). Sierra County: Loyalton*, 7 (Mailliard coll.). Placer County: 3 to 5 mi. E Truckee*, 7 (Moffitt coll.). Eldorado County: 9½ mi. S Phillips, 1 (Dickey coll.). Butte County: Oroville Y, west of Oroville, 1 (McLean coll.). Solano County: 6 mi. S Davis, 1 (McLean coll.).
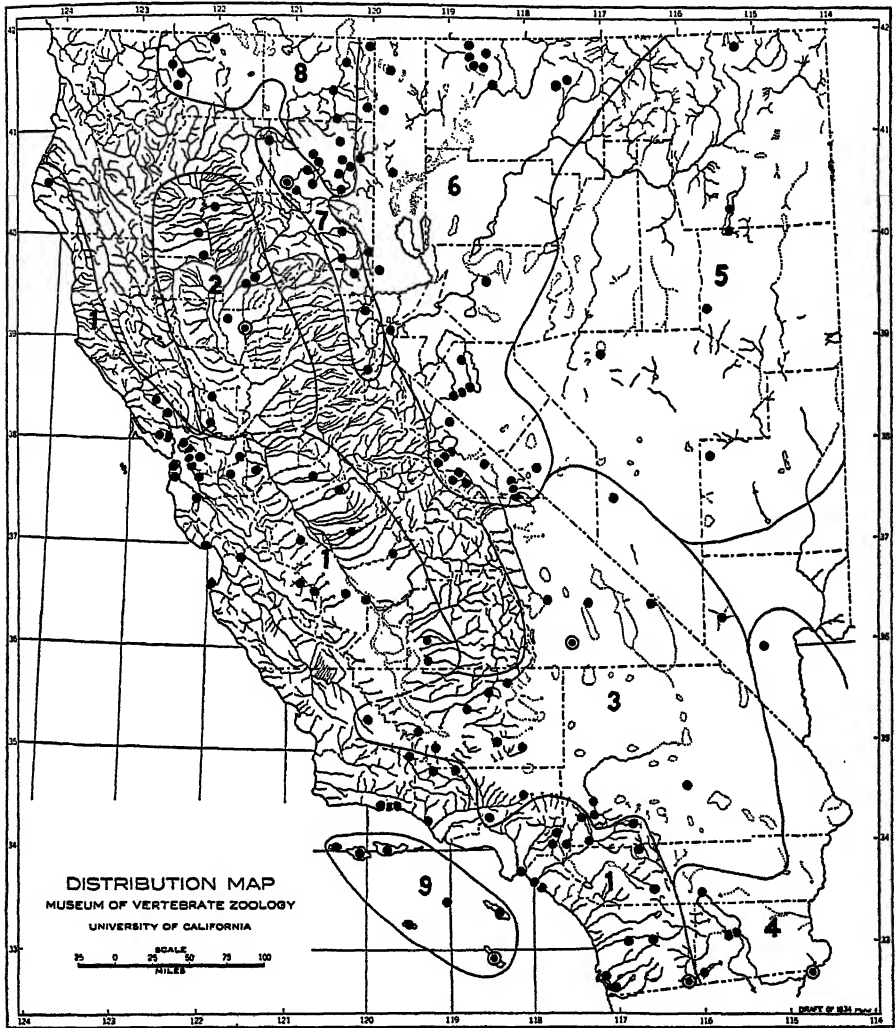

Fig. 4. Breeding ranges in California and Nevada of: 1, *O. a. actia*; 2, *O. a. rubea*; 3, *O. a. ammophila*; 4, *O. a. leucansiptila*; 5, *O. a. utahensis*; 6, *O. a. lamprochroma*; 7, *O. a. sierrae*; 8, *O. a. merrilli*; 9, *O. a. insularis*. Plain dots indicate localities from which breeding specimens have been examined; encircled dots indicate type localities.

Habitat notes.—Representatives of this race are to be found, over the greater part of their breeding range, only in large open meadows and flats such as are found here and there within heavy timber on the Sierra Nevada. Such suitable habitats are relatively few and are far separated. The open flats are for the most part free from shrubs and are only sparsely covered with grasses and "weeds." On the edges of such meadows and forming a wall around

them are towering Jeffrey pines (*Pinus jeffreyi*), white fir (*Abies concolor*), and incense cedar (*Libocedrus decurrens*). The range of *sierrae* is almost entirely within the Transition Life Zone. Owing to the fact that snow remains late on the breeding grounds, the time of nesting must be later than that of neighboring desert-inhabiting races; in all probability but one brood per season is raised, as compared with two or three in some races. Little is known about nesting dates or nesting activity of this race.

Members of the race *sierrae* are forced to leave their breeding grounds in the winter because of the heavy snowfall. Dates of migration are entirely unknown and few winter-taken examples are available. Two from the Sacramento Valley, one from near Oroville, Butte County, and the other taken 6 miles south of Davis, in Solano County, indicate a westerly movement to lower altitudes. On the other hand, it is highly probable that many drop down eastward to Honey Lake Valley and other desert locations in Nevada. Possibly some winter in Sierra Valley. Sight records of Mr. Donald McLean indicate that many winter in Honey Lake Valley. He has been able to detect yellow-bellied birds among the great flocks there in winter, which are a composite lot comprised of *sierrae, merrilli, lamprochroma,* and a few *arcticola*. It also seems that after the breeding season and before emigration, the Sierra Nevada horned larks congregate in large flocks on their mountain meadows, as at Gray's Flat where the Bogard Ranger Station is situated, at Last Chance Creek, and in Sierra Valley.

Nomenclatural history.—In his review of the horned larks, Oberholser (1902) found many peculiarities among representatives from the Sierra Nevada. The most notable thing about certain skins was the unusually great extension of yellow on the underparts. In addition, the coloring of the dorsum was such that the specimens did not fit in with *merrilli*, but rather seemed intermediate between *rubea* and *merrilli* and hence somewhat like *strigata*. In 1920, on the basis of eleven specimens, Oberholser formally described the race *sierrae*, assigning to it a range "in the region of the Sierra Nevada." Of the eleven specimens used as the basis for the description of this race, only four were breeding birds, and three of these (all taken on the same day) were from one locality—the type locality. The race *sierrae* was not only based on scanty material but the range ascribed to the race was vague and uncertain.

The type locality of *sierrae* is situated within the "Lassen Section" of Grinnell, Dixon, and Linsdale (1930). Collectors working on the survey of this section did not obtain specimens from the type locality although examples were taken at Champ's Flat on Pine Creek and at other points eastward. Of all the specimens taken, only one, these authors thought, seemed to conform to Oberholser's characterization of *sierrae*. This one was an October-taken bird from Champ's Flat. All the other specimens were considered as belonging to the race *merrilli*. On the basis of their material and the circumstances mentioned in connection with Oberholser's account, Grinnell, Dixon, and Linsdale were not convinced that the existence of a recognizable race "in the region of the Sierra Nevada" had been established. However, a study of the richer material which I have assembled now indicates that the race *sierrae* is one of the most

strongly differentiated of any of the races of horned larks. Enough skins are available to show that the race does have a definite range. Furthermore, it has been possible to ascertain certain areas of intergradation and to work out the relationships of the race *sierrae* with the neighboring races.

Distribution and variation.—Birds showing in most extreme degree the characters of *sierrae* are those from the region of the type locality. The yellow is most pronounced in these specimens and all the skins have the distinctive deep reddish brown dorsum. With the exception of intergradational specimens to be discussed later, all breeding examples of this race show a singular uniformity in their characters. In other words, the material at hand shows no differential trends in characters within the race—no local peculiarities. The single breeding male from near Pittville, the northernmost locality from which representatives of the race are at hand, is the same as those from Bogard and Last Chance Creek. It is also almost identical with those from the southernmost locality represented, which is just east of Truckee. The specimens from the last-mentioned locality were taken late in the season and appear somewhat lighter, but this is a result of fading and wear. Most of the yellow on the breast is gone from the Truckee specimens, but the underlying feathers show traces of yellow, undoubtedly indicating that yellow once suffused the entire lower surface.

The race *sierrae* presents many peculiarities of distribution. Since suitable habitats are relatively few and far between, the distribution of *sierrae* is markedly discontinuous. The restriction of the race to open flats within forested areas figures significantly in the geographic relations of *sierrae* to neighboring races. For instance, the presence of a continuously forested area on the western slope of the Sierra Nevada acts as an effective and apparently complete barrier between the breeding ranges of *sierrae* and *rubea*, preventing any intergradation between those two races.

Sierrae is separated from *lamprochroma* for the most part, too, by physical barriers, although intergradation does occur in at least one place. This is of interest, not alone because of the characters of the intermediates in the area of intergradation but also because of the part that the physiographic features play in the phenomenon.

The intermediate population in question centers in Sierra Valley, in Plumas County, California. Representatives are present from two localities there, Beckwith and Loyalton. All these skins are unquestionably referable to *sierrae* but show suggestion of an approach to the neighboring race *lamprochroma*. This tendency is most noticeable in the coloration of the back, which is lighter than in typical *sierrae*. The nape, occiput, bend of wing, and sides of breast are also of a lighter tone. The specimens from Loyalton are browner than those from Beckwith, but the former were taken in early June, whereas those from Beckwith were taken approximately a month later. The Beckwith series shows considerable wear, which, together with the intermediate characters, has resulted in a close resemblance to worn examples of the race *merrilli* from the Madeline Plains of Lassen County, California. None of these worn Sierra Valley birds show any strong yellow on the underparts.

Another fact in connection with the Loyalton series is the close similarity of dorsal coloring to that of the locally peculiar series from Yreka already discussed. Some individuals from the two localities can scarcely be distinguished, but, as a whole, the Yreka series has more yellow on the head, while the Loyalton series is a very little ruddier on the nape.

The fact that members of *sierrae* taken in Sierra Valley show an approach to *lamprochroma* is not surprising when one considers the geographic position. Sierra Valley is a relatively arid valley supporting vegetation of the Great Basin type. It is located at what might be called the eastern edge of the Sierra mountain mass. At this place there is no abrupt declivity on the east base of the Sierra Nevada as there is immediately to the northward. In fact, Sierra Valley, although in the mountains, is in close touch with the desert region to the east of the axis of the Sierra Nevada. Sierra Valley is separated from the neighboring valley to the east, Long Valley, only by a low pass known as Chilcoot Pass. Long Valley runs north and opens into Honey Lake Valley where *lamprochroma* is known to breed. It appears, then, that there is no complete barrier in the Sierra Valley–Long Valley region between *sierrae* and *lamprochroma*. Interbreeding or racial hybridization is therefore possible at this point, whereas, because of physical barriers, it would be impossible in most other places where the ranges of *sierrae* and *lamprochroma* approach.

A further consideration in connection with the Sierra Valley horned larks concerns the matter of zonation. The race *lamprochroma* seems restricted in the breeding season to the Upper Sonoran desert region at the east base of the mountains, while the race *sierrae* is confined to the Transition Zone of higher elevation. Sierra Valley is intermediate or overlapping between the two zones, and the horned larks from there are intermediate in their characters.

To the northward of Sierra Valley the mountains break off very suddenly on the east side, resulting in a steep declivity of several thousand feet. Below is Honey Lake Valley; above is Last Chance Creek. In the lower desert region at about 4000 feet elevation, breeding horned larks belong to the race *lamprochroma;* above, at approximately 7000 feet, they are of the race *sierrae.* In an air line, these two localities are extremely close together, but two very different environments are apparent in the two places, and a different race occupies each. There are obviously differences in humidity, temperature, rainfall, and vegetation. The sudden declivity of the mountains prevents any intermixture of the two races in the breeding season and thus forms an effective barrier. The line of demarcation between the ranges of these two races, then, follows along this eastern face of the Sierra Nevada where there is a very narrow, near-vertical intervening strip that is unoccupied by any horned lark.

In various places several fall and winter birds of unknown breeding locality have turned up which seem closest to the race *sierrae* but which are not at all typical. In fact, their appearance suggests that they may be intergrades between *sierrae* and *lamprochroma,* yet they in no way resemble the intermediates from Beckwith or Loyalton. There are five of these specimens. One of them is no. 44402, Mus. Vert. Zoöl., from Champ's Flat on Pine Creek,

Lassen County, an adult male taken October 18, 1923. This specimen was mentioned by Grinnell, Dixon, and Linsdale (1930:286) as being the only one of the skins collected in the Lassen survey that conformed to Oberholser's characterization of *sierrae*. Incidentally, of the other two from Champ's Flat mentioned by the authors just cited, the female, no. 44404, taken at the same time, is like the male under discussion here, no. 44402. A second male, no. 44403, is more blackish, and I have referred it to *merrilli*.

Another of these peculiar examples is from Merrillville, Lassen County, at the southeast side of Eagle Lake. This specimen, a male, no. 41548, Mus. Vert. Zoöl., was taken September 28, 1915. Others are no. E-402, Dickey collection, a male, taken October 2, 1917, at Corning, Tehama County, and no. 2259, Ellis collection, male, taken November 28, 1925, five miles east of Butte City, Butte County, California. These specimens are all characterized by much lighter backs than *sierrae*, but like that race they have deep ruddy on the occiput, nape, and bend of wing. Also, the underparts are heavily suffused with yellow. The dorsal feathers have brown centers and sometimes a suggestion of yellowish on the feather tips. From this evidence of some strong affinity with *sierrae*, it may be assumed that they came from some part of the periphery of the general range, probably a contact area with *lamprochroma* west or northwest of Honey Lake Valley. If they were intergrades between *sierrae* and *merrilli*, I would expect them to be considerably more blackish. The fact that they occur in the Eagle Lake region and also in the Sacramento Valley supports the theory that birds from the range of *sierrae* winter in part at least in the Sacramento Valley. Curiously, except for the yellow below, these intergrades are fairly similar to certain autumn intergrades between *actia* and *rubea* from Stockton and vicinity.

The single breeding specimen from Pittville is typical of *sierrae*. It seems probable, however, that the Fall River Valley marks the northernmost limits of the range of true *sierrae*. Specimens from the area of lava beds north of there show signs of intermediacy between *sierrae* and *merrilli*.

Our present understanding of *sierrae* clears up a heretofore ambiguous situation with reference to examples from Summit, Nevada County, California, as described by Oberholser (1902:835). Specimens from Summit which were previously considered intergrades between *merrilli* and *strigata* are now known to be examples of *sierrae*. Apparently, horned larks do not breed in the vicinity of Lake Tahoe, although there are some clearings at the south end of the lake that appear to afford a suitable habitat. Two birds collected there in the fall proved to be of the race *lamprochroma*. It is not known just how far south in the Sierra Nevada the range of *sierrae* extends. The southernmost locality whence breeding adults are present is 5 miles east of Truckee. However, in the Dickey collection is a juvenile, no. G-196 taken July 29, 1919, at 9½ miles south of Phillips, Eldorado County, California. This individual is probably referable to *sierrae*, although it is considerably lighter and much more tan-colored than the series of juveniles from Beckwith. It is decidedly darker than juveniles of *lamprochroma*, but not unlike certain ones of *actia*. I can conceive, however, of no possible intergradation between *actia* and

sierrae. Since juveniles often show an appreciable range of variation, it is most likely that this single example is an extreme of *sierrae* that happens to resemble certain extremes of the race *actia*.

Otocoris alpestris strigata Henshaw

Streaked Horned Lark

[*Otocorys alpestris*] *strigata* Henshaw (1884:261, 267), original description
Otocoris alpestris strigata, Dwight (1890:151), part; Bendire (1895:344); Bowles
    (1898:53); Bowles (1900:30); Oberholser (1902:837); Grinnell (1902:44);
    Macoun (1903:368); Ridgway (1907:316); Macoun and Macoun (1909:400);
    Dawson and Bowles (1909:217); Grinnell (1912:15); Grinnell (1915:94); Ma-
    coun and Macoun (1915:474); Dawson (1923:839); Brooks and Swarth (1925:
    77); Taverner (1926:254); Kitchin (1931:83); Taverner (1934:297)
Chionophilos alpestris strigatus, Hellmayr (1935:5)

Type.—Adult male, no. 8734, U. S. Nat. Mus.; Fort Steilacoom, Pierce County, Washington; April 15, 1856; collected by George Suckley. This locality is near the southern end of Puget Sound, between Tacoma and Fort Lewis.

Diagnosis.—In dorsal coloration somewhat like *merrilli* but less blackish, more brownish and with a brighter nape and bend of wing, smaller, and further differing in the possession of yellow on the underparts; more closely resembling *sierrae*, having yellow below as in that race, but dorsal coloring darker brown, with less ruddy and more contrast between nape and back; most closely resembling *insularis*, being comparable in size and general appearance but distinguished by having dorsum lighter, the breast region less heavily streaked, and underparts washed with yellow; distinguished from *actia* by darker coloration on upper parts and yellow below. The combination of small size, dark brown back, and yellow on the underparts serves to distinguish this race from all others. The color of the nape in typical specimens is best designated as Walnut Brown; the back is usually near Warm Sepia. The hue of the yellow on the underparts is variable.

Measurements (in millimeters).—Breeding males (7 specimens from northern part of range): wing, 96.9 (100.4–93.4); tail, 62.4 (67.0–52.4); bill from nostril, 9.3 (9.7–8.6); tarsus, 20.7 (21.5–20.2); middle toe without claw, 9.8 (10.8–8.7).

Breeding males (11 specimens from southern part of range in the Rogue River region of Oregon): wing, 100.2 (103.5–98.0); tail, 67.3 (70.2–64.0); bill from nostril, 8.9 (10.0–8.1); tarsus, 21.0 (22.0–19.8); middle toe without claw, 11.0 (11.7–10.4).

Breeding females (3 specimens): wing, 90.4 (91.2–89.8); tail, 57.2 (59.4–54.5); bill from nostril, 8.9 (9.8–8.2); tarsus, 19.9 (20.8–19.0); middle toe without claw, 10.7 (11.7–10.2).

Distribution.—Occurs during the breeding season along the coastal strip west of the crest of the Cascade Mountains in Oregon, Washington, and extreme southwestern British Columbia. In winter, some examples of this race presumably move south to northern California; some few are resident; others may move eastward to eastern Washington and Oregon.

Specimens examined.—Representative skins of this race total 37. Of these, 17 are breeding males, 3 breeding females, 9 autumn and winter males, 5 autumn and winter females, and 3 juveniles. These are from the following localities. Breeding birds are marked with an asterisk. Unless otherwise indicated specimens are in the Museum of Vertebrate Zoölogy.

BRITISH COLUMBIA.—Sumas Prairie*, 1 (Racey coll.); Lulu Island*, 1 (Racey coll.); Sea Island, 1 (Provincial Mus.), 1 (Racey coll.); Boundary Bay 1, (Brooks coll.); Victoria*, 1 (Provincial Mus.).

WASHINGTON.—Pierce County: Tacoma*, 4 (Dickey coll.); South Tacoma, 1; Spanaway, 2 (Dickey coll.); Parkland, 1 (Dickey coll.).

OREGON.—Linn County: Scio*, 2 (Jewett coll.). Polk County: Rickreal*, 1 (Dickey coll.). Clackamas County: Mulino*, 1 (Dickey coll.). Multnomah County: Portland, 1 (Dickey coll.). Marion County: Salem*, 1; 10 mi. N Salem*, 1; Woodburn, 1 (Jewett coll.). Jackson County: Medford*, 3 (Jewett coll.); 5 mi. N Medford, 1; 8 mi. NNE Medford*, 7; 3 mi. S Eagle Point, 2. Curry County: Goldbeach, 1 (Jewett coll.).

Habitat notes.—Members of this race are confined to the humid coast belt of the Pacific Northwest, a region of heavy rainfall, high humidity, and dense vegetation. The forests are made up of Douglas fir (*Pseudotsuga taxifolia*), Sitka spruce (*Picea sitkensis*), western red cedar (*Thuya plicata*), and coast hemlock (*Tsuga heterophylla*), with a dense forest undercover. In this region one sees to best advantage the effect on horned larks of heavy vegetation as a limiting factor. Near towns and cities, members of the race occupy rolling, open farming sections where much of the timber has been cleared away. Around Tacoma, Washington, fairways of golf courses are often frequented. Bowles (1898:53) found streaked horned larks about six miles from Tacoma where the dense woods change to open prairie. They occurred where the soil was dry and sandy and the vegetation was of short grass mixed with sparse clumps of small prairie ferns, which in large patches grow to a height of six or seven inches. Horned larks were local in their distribution, he stated (1900:30), large areas of prairie being altogether untenanted, whereas seemingly similar pieces of land would be swarming with them. Near the sea front they are found in moss-covered tracts and on barren, semirocky slopes. In the Vancouver region, members of the race occur in areas that have been cleared of timber, and in drained swampland or reclaimed areas that have been filled in. Nesting begins, according to Bowles (1900:30), in late April. The nesting season extends through the first week in July, with the height of the season about the middle of May. Probably two broods per year are raised.

Distribution and variation.—The race *strigata* was among the first races recognized, but there has been much confusion with respect to the extent of its range. Dwight considered that its range included the Santa Barbara Islands off the coast of California. Indeed, the resemblance, as will be seen later, is strikingly close between Oregon *strigata* and the birds that breed on the islands and are now known as *insularis*. In his monograph, Oberholser suggested that the breeding horned larks of the high meadows in the Sierra Nevada were probably referable to this race. Even though the breeding birds of the northern part of the Sierra Nevada are subspecifically different, they, too, closely resemble *strigata*. However, as at the present moment understood, *strigata* has a range that is much the same as the one Henshaw originally gave it. Thus the history of treatment of the race has been one of expansion of range and subsequent reduction.

In breeding range, *strigata* appears to be restricted, by physical boundaries, to the humid coast strip of the Pacific Northwest, this strip lying altogether west of the main crest of the Cascade Mountains. It does not come in contact with other races to any great extent on its southern margin. Because of the generally forested aspect of the country, the areas of actual occurrence are themselves isolated. This discontinuity of range, is, as far as I know, shared in like degree only with one other race, *sierrae*, which also occurs in forested country. Probably as a result of this feature, the aggregate number of individuals of this race is not as large as that of races occurring in continuously open country.

It seems to me likely that the internal pressure in the population of *strigata*

is greater, perhaps, than in other races. At the same time, because of the restriction in available habitat, and of the presence of other limiting factors such as the Cascade Mountains which prevent eastward expansion, the race is not able to push beyond its present boundaries. It would seem, therefore, that expansion of the race apparently cannot occur except as changes within the general range take place which make available more habitat suitable for horned larks. Such changes of recent years have occurred chiefly through the agency of man. Although the extent of man's activity in affecting the race is for the most part unknown, one example has come to my attention that illustrates the point.

In southwestern British Columbia in the Chilliwack region, some fifty miles east of Vancouver and just north of the international boundary, there existed until a few years ago a lake and swamp known, respectively, as Sumas Lake and Sumas Prairie. The latter was a flat alluvial plain covered with grass. It was intersected by winding sloughs and was usually inundated each year by the rise of the Fraser River in June and July. These were the conditions prior to at least 1894, as described by Brooks (1917:29). This area has recently been drained, cleared, and given over to agriculture. During all the years that Major Brooks made collections and intensive observations on the birds in this region, from 1887 to 1894, he has not a single record of horned larks nesting there. Nor are any nesting data given by Brooks and Swarth (1925:77). Yet in more recent years, horned larks belonging to this race have come to be found regularly in the Chilliwack region; that area is now suitable for them. They first appeared about 1926, according to Major Brooks, and nest there now. In the Racey collection is a breeding male taken July 14, 1929, at Sumas Prairie. This extension of range is apparently a result of the occupation of a newly available area by birds forced into it by population pressures within the race.

Elsewhere within the range of *strigata,* changes resulting from clearing and cultivation of land and reforestation of open areas probably have caused many local shiftings of population. Changes of this sort have been especially noticeable in recent years around South Tacoma and Fort Lewis, Washington. About the only places where *strigata* seems to be at all numerous are the South Tacoma region and the region south of Vancouver, B.C. Dawson and Bowles have made the statement that in the state of Washington *strigata* is confined chiefly to prairies in Pierce, Thurston, and Chehalis counties.

It is of interest to note in passing that Henshaw did not assign *strigata* to the extreme southwestern part of British Columbia. Dwight did so, but with some question. Oberholser did not include any part of British Columbia in the range of *strigata.* Yet today, as indicated by the specimens listed, there is no doubt that the extreme southwestern part of British Columbia is to be included in the breeding range of this race.

Certain misgivings have arisen also concerning the southernmost limits of the breeding range of *strigata.* Grinnell (1931:74) referred breeding specimens from Humboldt County, California, to this race. I have examined these specimens and consider them to be of the race *actia* despite the fact that they were taken in the humid coast belt. Skins from Humboldt County are dis-

cussed in detail under *actia*. They do not appear to me to be even intermediates between the two races.

The examples of *strigata* with darkest dorsal coloration are from the extreme northern part of the range. The breeding male mentioned above from Sumas Prairie stands out because of its decidedly blackish back, and in this one character it shows an approach to *merrilli*. Its small size and brightly colored nape and bend of wing, however, leave no doubt as to its identity with *strigata*. From farther south, specimens are more brownish, less blackish. The central parts of the back feathers are darker than the edges, sometimes producing a slight streaked effect. This is, however, no more noticeable than in *merrilli* and many other races. There is less appearance of streaking in examples from the southern part of the range because the dorsal feathers of such birds are more uniformly brown.

The smallest specimens are found in the northern part of the range, where the wing length of seven breeding males averages 96.9 mm. A tendency to larger size in specimens from the southern part of the range is shown by specimens from Medford, Oregon, eleven males of which average 100.2 mm. In this character the southern birds show an approach to *merrilli*. With reference to the presence of small-sized, otherwise typical, *strigata* in the northern part of the range, we have a reversal of the usual rule among birds of North America that specimens from the northern part of a range are of the same size or larger than those at the southern end.

One other character that shows variation within the race is the amount of yellow coloring the underparts. Yellow on the underparts is not uniformly present in examples of the race, but the highest frequency of occurrence is in birds from the Puget Sound region. Examples from the southern part of the range lack this yellow for the most part. The skin at hand with the greatest amount of yellow beneath is a male in the Brooks collection taken in December at Boundary Bay, British Columbia.

The presence of yellow pigment on the underparts has been variously weighted by different reviewers of the species with respect to its value as a subspecific character. In his original description, Henshaw emphasized the presence of yellow. Dwight concluded that the type specimens were abnormal in this respect and stated that an equal amount of yellow was to be found in other races, particularly *merrilli*. Oberholser, on the other hand, remarked (1902:839), "There is much variation in the amount and intensity of the yellow in this race, which color is seemingly seldom, if ever, wholly lacking in either sex." This character of yellow below should not, in my opinion, be slighted. It is a mark of distinction for *strigata* and occurs extensively in only one other race, *sierrae*. This might be interpreted as evidence of relationship between these two races. Individuals of *merrilli* with yellow on the underparts are of rare occurrence and when present probably have resulted from crossings between *merrilli* and *strigata*, although no area of contact between *strigata* and *merrilli* is at present definitely known. It may well be that in isolated meadows along the Cascade Mountains there exist populations made up of representatives of both *merrilli* and *strigata* stock that somehow have

come together. The intermediate winter specimens at hand strengthen the supposition that such areas occur. This yellow, as a character, will bear closer examination in the future from a genetic standpoint when more material is available and when more is known of the contact areas of the races involved.

Thus the area wherein the most typical specimens of *strigata* occur extends from the Puget Sound region south to Salem, Oregon. Birds from this area, particularly from Tacoma and vicinity, are the smallest representatives of the race, their backs are consistently dark brown, and the nape and bend of wing are more highly colored than in any other examples of the race. Examples from this region also have the characteristic yellow color. North and south of this metropolis the birds become slightly different in their appearances, and one or two trends in certain characters are noticeable in a north-south direction. The range of the race is so narrow and specimens at hand so few that no east-west trends are detectable, if, indeed, such exist.

One of the peculiarities of *strigata* is the presence of a well-defined migratory movement. One might expect this race to be more or less sedentary, because the area in which it is found breeding does not experience severe winters. The late J. H. Bowles, who has written much on the streaked horned lark from his observations in the Tacoma region, has stated (1898:53) that they suddenly leave the region about the middle of October or earlier. He also states that they usually arrive about the fourth week in March, coming suddenly in large numbers. In a later publication (1900:30) he states that they may arrive as early as the latter part of February and are often already in pairs. However, some few do winter over in their breeding range. Oberholser (1902:839) cites a winter record for Colton, Whitman County, Washington, and states that *strigata* occurs east in winter to eastern Oregon and Washington. Yet, Dawson and Bowles (1909:214) say that "much clearer testimony is required on this point." Dawson apparently never observed the form in Yakima County, and the authors just cited further state that " . . . it would seem remarkable that a bird should forsake the mild climate of Tacoma to endure the more severe winters and less certain food supply of the East-side [of the Cascades]."

Several authors have referred winter specimens from various points in northern California to this race. A certain doubt must be attached to most of these records, however, because of the likelihood of confusion of *strigata* with *sierrae*. Since examples of both these races winter in northern California and since the two races show a close resemblance, some of these records of *strigata*, particularly the older ones, doubtless refer to *sierrae*. In this connection, Oberholser stated (1920:35) when he described *sierrae* that ". . . specimens recorded by the writer from Red Bluff and San Francisco . . . are true *Otocoris alpestris strigata*." In the material I have had for examination there are no examples of *strigata* from California. Certain wintering examples from the Sacramento Valley show a likeness to *strigata,* but they are too large and the females lack the usual intensified color on the bend of the wing. These specimens seem, rather, to have come from the Columbia River region in eastern Oregon and Washington, and hence are *merrilli.*

Otocoris alpestris insularis Dwight

Island Horned Lark

Otocoris alpestris strigata, Dwight (1890:151), part
Otocoris alpestris insularis (Townsend MS) Dwight (1890:152), original description:
  Townsend (1890:140); Bendire (1895:347); Oberholser (1902:839); Ridgway
  (1907:317); Grinnell (1912:16); Grinnell (1915:95); Howell (1917:67); Daw-
  son (1923:838); Dickey and van Rossem (1924:110); Grinnell (1932:286);
  Willett (1933:111)
Otocoris insularis, Grinnell (1902:45); Linton (1908:127)
Chionophilos alpestris insularis, Underdown (1931:441); Hellmayr (1935:6)

Type.—Adult male, no. 117674, U. S. Nat. Mus.; San Clemente Island, Los Angeles
County, California; January 25, 1889; collected by Charles H. Townsend.

Diagnosis.—Most closely resembles *strigata* but differs from that race in being darker
above with a brighter tone on the nape, without a yellow wash on the underparts, and by
being more heavily streaked on the breast; distinguished from *actia* by the very much darker
coloration throughout, heavier streaking below, more intensive pigmentation on the nape,
and broader bill at base. In fresh-plumaged average specimens, the nape is Chestnut Brown,
the bend of wing Auburn, sides of chest Chestnut or Bay, and back Fuscous. These colors
are accentuated with wear of the feathers.

Measurements (in millimeters).—Breeding males (42 specimens): wing, 95.9 (99.3–90.2);
tail, 64.1 (67.4–57.7); bill from nostril, 9.3 (10.1–8.2); tarsus, 21.1 (22.3–19.3); middle
toe without claw, 10.6 (11.8–9.7).

Breeding females (26 specimens): wing, 89.2 (93.5–84.5); tail, 56.4 (60.0–53.4); bill
from nostril, 8.6 (9.2–7.6); tarsus, 20.6 (21.7–19.2); middle toe without claw, 10.3 (10.9–9.4).

Distribution.—Breeds on all of the Santa Barbara or Channel islands, the archipelago
off the coast of southern California. In winter, members of the race apparently are regu-
larly found on the adjacent mainland as well as on the islands.

Specimens examined.—Skins which I have examined representative of this race total 188.
Of these, 68 are breeding males, 42 breeding females, 44 autumn and winter males, 24 autumn
and winter females, and 10 juveniles. These are from the following places. Breeding speci-
mens are marked with an asterisk. The place of deposit of the specimens is indicated.

CALIFORNIA.—Santa Barbara Islands. San Miguel Island: 24 (Mus. Vert. Zoöl), 3
(Dickey coll.). Santa Cruz Island*: 2 (Mus. Vert. Zoöl.), 10 (Dickey coll.), 1 (A. H. Miller
coll.), 22 (Mailliard coll.). Santa Barbara Island*: 4 (Mus. Vert. Zoöl.), 7 (Dickey coll.),
6 (Mailliard coll.), 2 (Calif. Acad. Sci.), 3 (A. H. Miller coll.), 1 (Law coll.). San Nicolas
Island*: 13 (Mus. Vert. Zoöl.), 9 (Dickey coll.), 3 (Mailliard coll.), 1 (Calif. Acad. Sci.),
1 (Law coll.). San Clemente Island: 8 (Mus. Vert. Zoöl.), 39 (Dickey coll.), 8 (Calif. Acad.
Sci.), 5 (Mailliard coll.), 5 (Law coll.).

Mainland. Santa Barbara County: Goleta, 1 (Dickey coll.). Ventura County: Sea coast
in vicinity of Oxnard, 1 (Dickey coll.). Los Angeles County: Long Beach, 3 (Dickey coll.).
Orange County: Anaheim Landing, 1 (Dickey coll.). San Diego County: San Diego, 1 (Law
coll.); Imperial Beach, 3 (Law coll.), 1 (Dickey coll.).

Habitat notes.—The islands upon which this race occurs offer a variety of
habitats, but true to their inherent requirements the horned larks frequent
the barren or short-grass mesas and open uplands. Dickey and van Rossem
(1924:110) make the statement that "on the Santa Barbara Islands, the race
is found almost exclusively on upland pasture lands." Most of the mainland
record-specimens were taken on the sand dunes just back of the ocean beach.

According to Howell (1917:13), the island habitat is characterized by
slightly less rainfall than the mainland but is more humid because of the influ-

ences of ocean and fog. The climate is presumably comparatively uniform the year around. Howell (*op. cit.*:15) has also made the general statement, apply-ing to all nesting birds on the islands, that under conditions of the insular environment there is an advancement of events in the yearly cycle a month or more over those for most of the nearby mainland races. He collected juvenal horned larks during the last week in March. The island nesting dates for horned larks, however, are probably little if any different from those on the mainland, for Grinnell (1898:31) has found nearly fledged young in the Pasadena region the last week in March. Howell, after summarizing the nest-ing data, concluded that the island subspecies must raise at least three broods in a season. This is also true on the mainland.

Distribution and variation.—I have not listed all the Santa Barbara Islands as breeding localities for the race because there are no representatives in my material from Santa Rosa, Anacapa, and Santa Catalina islands. However, horned larks do occupy all the islands, for Oberholser (1902:841) lists Santa Catalina and Santa Rosa islands as being breeding localities, and Burt (1911: 164) mentions horned larks as abundant on Anacapa Island. No examples of this race occur on any of the other islands off the coast of California or Lower California. The specimen from Natividad Island thought by Lamb (1927:70) to be of this race is an example of *enertera*.

The race *insularis* is by no means a homogeneous one either with respect to individual variation or to intraracial geographic variation. There is as much individual variation present as one encounters in most of the mainland forms. In any large series present from a single island there are light brown extremes and more blackish extremes, with all manner of intermediates. By way of this individual variation there is intergradation not only with *actia* but also with *strigata*. Oberholser (1902:841) has stated that "Birds from the islands of San Miguel, Santa Rosa, and Santa Cruz, as compared with those from the more southern islands, appear to average slightly darker above, both on the nape and back, but this difference is too slight and inconstant to be worthy of more than passing notice. These dark birds represent the maxi-mum differentiation of *insularis*, while the birds with the rather paler napes and more brownish, less blackish backs, carried to apparently the greatest extreme on Santa Catalina Island, incline toward *actia*, and indicate the main-land origin of this insular form." Ridgway simply repeated these statements and in turn was quoted by Howell and by Willett.

My material gives no indication that the characters of the race are any more pronounced in the northern group of islands than in the more southern one. Nor is there any indication that the specimens from the southern islands incline toward those of the mainland. My largest series of breeding birds, how-ever, is from San Clemente Island, and there are few breeding specimens from the northern group for comparison. Conversely, most of my fall representa-tives are from the northern islands, and there are few examples in fresh fall plumage from the southern group. Nevertheless, five males in fresh fall plumage from San Clemente Island are not different as a group from a much larger series of autumn birds from San Miguel Island. Neither do breeding

specimens from the various islands represented show any differences. Since specimens in all stages of plumage from all the islands show great individual variation, comparison of only a few individuals might lead to erroneous conclusions.

There does not seem to be any correlation between distance from shore and degree of difference between races, such as Grinnell (1928) found for birds in general off the coast of Lower California. Specimens from Santa Barbara Island and Santa Cruz Island are as dark as those from San Miguel and San Nicolas islands.

It is a significant fact that almost everyone who has studied the systematics of the race *insularis* has been impressed with the likeness of the island birds to those from the Pacific Northwest representing the race *strigata*. Dwight, it will be recalled, did not give *insularis* subspecific status at all, for he considered horned larks from the islands to be the same as those from the range of *strigata*. Oberholser, after indicating his belief that *insularis* originated from *actia,* the mainland form, stated (1902:841) : "That *insularis* should have been differentiated toward *strigata* is, however, an interesting case of parallel development." Ridgway, as I have already mentioned, quotes from Oberholser. Howell, having quoted the passages from Ridgway that the characters of the race were best developed on the more northern islands whereas specimens from the southern group approached *actia,* states (*op. cit.*, p. 67) : "This would probably indicate that the island form originated from the latter [*actia*], but the more northern islands, having a damper climate, would tend to create characters more closely approaching those of *strigata* of the humid northwest."

With reference to these facts and interpretations, I cannot see that the overlap of certain characters (which show great individual variation in each race) in *insularis* and *actia* must be interpreted as evidence that *insularis* was derived from *actia*. I do not believe, either, that the likeness between *insularis* and *strigata* must be explained by parallel development. It seems to me that the close similarity of *insularis* and *strigata* has a deeper significance than has generally been credited to it. A more rational explanation of this similarity between the two races is that they were both once parts of a common ancestral stock. Having been separated in the course of time by physiographic changes, the two sections have become subspecifically different, but they still show certain definite marks of relationship. The evidence to support this theory is discussed in the section on subspeciation in horned larks (pp. 301–303).

It might be expected that the population of each island would show slight differences that might be attributed to the factor of isolation. No evidence of this sort has come to light, although if large and comparable series were present, slight differences might be revealed. The apparent lack of geographic variation from island to island within the range of *insularis* may result from several causes. In the first place, the islands are fairly close together and it is possible that horned larks cross from one island to another with such frequency that any inbreeding is prevented. I believe this to be true for the northern group of islands, and it probably holds as well in the southern group. There is room for doubt, though, whether there is much passage between the northern

and southern islands. The effectiveness of ocean stretches as barriers to the distribution of the island inhabitants probably varies in general with the breadth of those stretches.

Another factor is the uniformity of the environmental conditions to which horned larks are exposed on the islands. We would expect this to be fairly great, for even though the physical features of the islands differ, the horned larks are rather restricted in their habitat requirements and the more general factors, such as amount of fog, rainfall, cloudiness, temperature, and the like, are probably comparable on all the islands. General uniformity of environmental conditions would probably be conducive to uniformity in the insular populations.

Yet one other consideration presents itself, namely, that the populations on the different islands may not have been isolated for a sufficient time to show any incipient differences among themselves. One can attach little significance to this suggestion for the reason that, if there has been time enough for the insular form to differentiate from some mainland stock, there would also have been time enough for differentiation to take place on each island, provided that there was no intermingling of populations and no swamping of characters. It seems to me that the time factor cannot be relied upon in explaining the lack of differentiation among the different islands. The explanation probably lies either in uniform environmental conditions that are not conducive to differentiation, or in exchange of breeding stock between the islands.

Howell has found that birds in general breeding on the Santa Barbara Islands show certain differences in common that differentiate them from the mainland forms. He writes (1917:16) as follows: "Taking a composite of the lot, we find that the influences of this group of islands tend to produce a bird of greater total length, with larger, heavier bill, and heavier tarsus and foot. The length of wing and tail remains about the same, and coloration becomes darker, with brighter colors and heavier streaking." How do horned larks conform to these generalities? Specimens of *insularis* have smaller wings and tail than the mainland forms *strigata* and *actia*. The tarsus and middle-toe measurements average longer, and the bill is wider at the base and heavier. The colors are darker in general, particularly on the back. The color of the wing, nape, and occiput is decidedly brighter than in many other races, and the streaking on the breast is pronounced. The race *insularis* seems, then, to fit in well with this composite trend described by Howell.

As only eight juveniles of *insularis* have been available for examination, little can be said of variation in birds of this age. Four of those present are from San Clemente Island, the other four from Santa Barbara Island. Two of those from San Clemente, collected on March 23, 1918, show their very young age by the downy filaments adhering to the juvenal feathers. The juvenal rectrices are not fully grown. The four from Santa Barbara Island were taken late in May, and some show the very beginnings of postjuvenal molt. In general, the juveniles are dark, but not so dark as examples of *arcticola* and *strigata.*

One of the most interesting aspects of the distribution of *insularis* has to do

with the extent and frequency of its occurrence on the mainland. Do members of this race occur there only casually or does a regular shoreward migration take place in winter? At what points along the mainland does *insularis* occur in winter? Do examples of this race ever breed on the mainland? Many questions such as these arise, and although they cannot be answered completely, a considerable amount of data is at hand pertaining to these points.

The occurrence of *insularis* on the mainland was first reported by Linton (1908:181), who obtained a male on "December 4" [= January 18], 1908, from a large flock at Alamitos Bay, Los Angeles County. Howell (1917:67) mentioned this in his paper on the birds of the Santa Barbara Islands and stated: "It may be a regular winter visitant to the mainland coast, but I think it more likely that this bird was either an individual that had accidentally wandered from the islands, or a case of unusual variation of *actia*." Dickey and van Rossem (1924:110) reported two additional mainland records for *insularis*, a male taken November 26, 1915, at Goleta, Santa Barbara County, and another male, taken· August 22, 1922, near Oxnard, Ventura County. Willett (1933:111) reported, in addition to the records noted above, that twenty-one specimens of *insularis* were obtained by Dr. Bishop at La Patera Point, near Santa Barbara, between November 6 and December 10, 1918. The flock from which these specimens were taken was small on November 6, contained more than one hundred birds by November 14, and several hundred on December 3. It had decreased to eight or ten by December 12, and only two were seen December 17.

I have not seen the specimen recorded by Linton, nor have I examined those taken by Bishop. The two recorded by Dickey and van Rossem, nos. CX45 and K-534, Dickey collection, from Goleta and Oxnard, are indeed dark enough to be considered members of the island race. Other examples from the mainland in this same category were present in my assembled materials. Three additional specimens in the Dickey collection, nos. 23991, 23996, and 25261, all taken January 30, 1914, at Long Beach, Los Angeles County, are very dark, as is one, no. 10036, from Imperial Beach, San Diego County, California, taken August 12, 1914. Certain similar examples now in the Law collection, taken at the same time as the Dickey specimen from Imperial Beach, are nos. 2151, 2152, and 2156. One other equally dark example in the Law collection, no. 2155, was taken August 20, 1914, at San Diego. Considering the dark coloration of all these specimens and the fact that all were taken along the ocean front at mainland points nearest the islands, one would be inclined to assign them to *insularis*. The fact that equally dark specimens are to be found as extremes in series of *actia* from points far removed from the ocean front, however, necessitates caution.

In a large series of topotypical specimens of *actia*, taken at Jacumba, San Diego County, August 23, 1914, two specimens are as dark as examples of *insularis*. Yet all manner of intergrades are present between these extremes and birds typical of *actia*. Thus there is intergradation between *actia* and *insularis* in overlap of characters resulting from individual variation, even if not by actual interbreeding. Even though I have listed the coastal specimens

as *insularis,* there remains the possibility that such mainland examples resembling *insularis* may be extremes of *actia.* The fact that so many of these mainland examples of supposed *insularis* have been taken along the coast leads one to wonder whether the coastal influences are in some way responsible for the increased pigmentation and also whether there may not be some actual blood relationship as a result of interbreeding between members of *actia* and *insularis* along the coast front.

Although obviously much remains to be ascertained with respect to the relationships between *actia* and *insularis,* it seems that the occurrence of birds like the latter on the mainland is much more common than was originally supposed. There is some indication that large flocks of *insularis* occur on the mainland in winter, but whether there is any appreciable migratory movement shoreward remains to be definitely ascertained.

The question of whether examples of *insularis* breed along the mainland coast is indeed pressing. There are as yet little satisfactory data on this point, but the presence of molting examples from Imperial Beach, taken as early as August 12 and dark enough to be called *insularis,* indicates that they might do so. Also, a male taken at Anaheim Landing, Orange County, on March 28, may have been a breeding bird.

Otocoris alpestris rubea Henshaw

Ruddy Horned Lark

[*Otocorys alpestris*] *rubeus* Henshaw (1884:260, 267), part, original description
Otocoris alpestris rubea, Belding (1890:105); Dwight (1890:150); Bendire (1895:
  343); Oberholser (1902:851); Grinnell (1902:44); Ridgway (1907:322); Grinnell (1912:15); Grinnell (1915:94); Dawson (1923:838); Grinnell, Dixon, and Linsdale (1930:284); Grinnell (1932:285)
Eremophila alpestris rubea, Neumann (1927:376)
Otocoris berlepschi, Neumann (1927:376); Palmer (1928:269)
Chionophilos alpestris rubeus, Hellmayr (1935:7)

Type.—Adult male, no. 76599, U. S. Nat. Mus.; Marysville, Yuba County, California; February, 1878; collected by Lyman Belding.

Much confusion has existed in times past about the type locality of this race. Henshaw (1884:267), at the time of his original description, accepted the data on the label of the specimen chosen as the type, which read Stockton, California. Dwight did not question this. Oberholser also recorded the type locality as Stockton, California, although he pointed out that specimens from there were intermediate between *actia* and *rubea,* that the locality was queried on the label, and that therefore there was reason to believe that the type specimen had not come from Stockton. Ridgway repeated the facts as Oberholser had pointed them out. Finally, Grinnell (1932:285) showed that the type specimen was not collected at Stockton but was listed by Belding (1879:423) as having been taken at Marysville, Yuba County, California, thus definitely establishing the type locality of the race.

Diagnosis.—Similar to *sierrae* but smaller, brighter ruddy, with less dark brownish, and without yellow below; differs from *actia* only in more ruddy dorsal coloring; distinguished from *strigata* in that the back is more ruddy, the nape and back are continuous in color or nearly so, and there is a lack of any streaking or yellow on the underparts; smaller than *merrilli* and lacking the latter's blackish appearance. The uniformly colored ruddy brown dorsum, with little or no contrast between rump, back, and nape, constitutes the most conspicuous character of the race. A typical specimen in winter plumage has the nape Auburn

and back Argus Brown. Other individuals have a dorsal coloring near Prout Brown and Cinnamon Brown. In very worn and faded specimens the back is near Hazel.

Measurements (in millimeters).—Breeding males (29 specimens): wing, 97.3 (101.6–93.1); tail, 65.5 (70.8–62.3); bill from nostril, 8.8 (10.0–8.0); tarsus, 20.9 (21.9–19.5); middle toe without claw, 10.6 (11.7–9.4).

Breeding females (18 specimens); wing, 90.9 (95.8–87.5); tail, 58.8 (61.3–55.2); bill from nostril, 8.3 (9.0–7.7); tarsus, 20.3 (21.4–19.3); middle toe without claw, 10.3 (11.4–9.6).

Distribution.—Resident in the Sacramento Valley of California. The boundaries delimiting the range coincide with the bases of the mountains surrounding the valley except to the south where it breeds as far as Suisun Bay and intergrades with *actia* in the vicinity of Stockton.

Specimens examined.—Skins examined of this race total 172. Of these, 41 are breeding males, 28 breeding females, 65 winter and autumn males, 29 winter and autumn females, and 9 juveniles. These were taken at the following localities, all in California. Those localities where breeding birds were taken are marked with an asterisk. Unless otherwise indicated, specimens are in the Museum of Vertebrate Zoölogy.

CALIFORNIA.—Tehama County: Coyote Creek, 6 mi. S Red Bluff*, 3; 6 to 7 mi. SW Red Bluff, 2; Corning, 7 (Dickey coll.); 8 mi. S Corning, 13; 5 mi. N Orlando, 1; Dales, 600 feet, on Paine's Creek*, 9; 2 mi. N Dales, 8. Glenn County: 3 mi. E Norman, 15. Butte County: Dry Creek, 10 mi. NE Oroville*, 15; Chambers Ravine, 4 mi. N Oroville*, 11; 6 mi. W Oroville, 30; 1 mi. S Oroville Y, west of Oroville, 3 (McLean coll.). Sutter County: Marysville Buttes*, 12. Colusa County: 5 mi. E Maxwell, 1. Yolo County: Elkhorn Ferry, 7 mi. E Woodland, 6. Solano County: 3 mi. E Vacaville, 1 (Dickey coll.); 4 mi. SE Suisun*, 4; Putah Creek*, 1. Sacramento County: Elkgrove*, 1; Folsom City, 6 (Dickey coll.). Amador County: Carbondale, 9 (Dickey coll.); 5 mi. W Drytown*, 13 (Mailliard coll.).

Habitat notes.—Members of the race *rubea* occur both in summer and winter on the dry plains and fields of the floor of the Sacramento Valley and also on the rolling foothills covered with grassland vegetation. Preference seems to be shown for gravelly areas. Since much of the country is given over to orchards and pasture land, the range of *rubea* is small; nevertheless the larks are abundant. It is a noteworthy fact that the substratum in much of their range is of a ruddy hue, forming a background against which the birds when motionless are inconspicuous. The hot dry conditions make for permanent residence, early nesting, and probably three broods per year.

Distribution and variation.—On all sides except one, the distributional range is delimited by the forests and mountains which skirt the Sacramento Valley. Contact with any of the surrounding races is therefore barred except to the south, where the Sacramento Valley is continuous with the San Joaquin Valley, the two together forming the so-called Great Valley of California. Intergradation between *rubea* and *actia* occurs over a large area in the central part of the Great Valley.

The most typical examples of *rubea* come from the area about Red Bluff, Tehama County, and Oroville, Butte County, California. Here the breeding birds and autumn examples in fresh plumage are the most ruddy. However, elsewhere the departure in color is but slight. It can be said in general that radially from the metropolis, examples become progressively a trifle less ruddy. This tendency is seen principally in the color of the central part of the individual back feathers, but also to less extent in the feather tips.

There is some variation in the distance that the ruddiness of the head and nape extends down onto the back. In some specimens it grades down to the middle of the back; in others it stops just posterior to the nape. The examples from the Oroville region seem to be characterized by extension of the ruddy far down onto the back, with no break in color between back and nape. On the other hand, a series of birds taken in the vicinity of Norman, Glenn County, in late February when they were on their breeding territories, have browner backs which show more contrast with the ruddiness of the nape and occiput.

Aside from the intensification of red in specimens from the center of differentiation, there is no other geographic variation within the race except that having to do with the southward merging of *rubea* into *actia*. The most northerly specimens at hand that indicate this transition are those from Elkhorn Ferry, 7 miles east of Woodland, Yolo County. Several males, females, and juveniles in various stages of molt, all taken in early September, are slightly less ruddy than specimens from farther north. These birds might reasonably be expected to have been on or near their breeding grounds when collected. If they were, this indicates the beginning of the southward trend toward *actia*.

An example from Putah Creek, and others from 4 miles southeast of Suisun, Solano County, are closest to *rubea*, although approaching *actia*. Specimens taken in early August at Byron Hot Springs, and others in fresh plumage from Stockton, are definitely intergrades between *actia* and *rubea*, perhaps slightly closer to *actia*. Because of the gradual blending of the two races in the center of the Great Valley, it is impossible exactly to mark division of their ranges. Suisun Bay and the Sacramento River as far as the junction with the San Joaquin River probably form somewhat of a barrier. If we draw a line eastward from here across the valley to the Sierran foothills we can indicate a more or less arbitrary division.

Rubea is a resident race. There is undoubtedly wandering between breeding seasons, but it seems very unlikely that this carries birds outside of their breeding range.

Otocoris alpestris actia Oberholser

California Horned Lark

[*Otocorys alpestris*] *rubeus* Henshaw (1884:260, 267), part
Otocoris alpestris rubea, Bryant (1889:292)
Otocoris alpestris chrysolaema, Dwight (1890:149), part; Belding (1890:105); Anthony (1893:238); Bendire (1895:341), part; Grinnell (1902:44)
Otocoris alpestris pallida, Anthony (1893:238); Bendire (1895:341), part
Otocoris alpestris strigata, Mailliard and Mailliard (1901:120); Grinnell (1931:74)
Otocoris alpestris actia Oberholser (1902:845), original description; Ridgway (1907: 320); Grinnell (1908:82); Grinnell (1912:15); Willett (1912:66); Tyler (1913: 62); Grinnell and Swarth (1913:206); Grinnell (1915:94); Nelson (1921:130); Dawson (1923:837); Grinnell and Storer (1924:374); Grinnell and Wythe (1927: 100); Grinnell (1928:143); Grinnell (1932:286); Willett (1933:112)
Otocoris alpestris insularis, Lamb (1927:70)
Chionophilos alpestris actius, Hellmayr (1935:6)

Type.—Adult male, no. 133678, U. S. Nat. Mus.; Jacumba, San Diego County, California; May 23, 1894; collected by Edgar A. Mearns, original no. 10920.

Diagnosis.—Similar to *rubea* in size and general coloration, but less ruddy and with more contrast between nape and back; darker, more brownish than *ammophila* but similar in size;

differs from *leucansiptila* by being darker and slightly smaller; also darker and larger than *enertera;* lighter, more ruddy than *strigata*, and lacking all yellow on breast and underparts; smaller than *lamprochroma* and with dorsal coloration brighter brown, not grayish. A typical male in early breeding plumage has a dorsal color that is Rood's Brown, while the nape is Pecan Brown. Unworn and unfaded plumages are brighter and the colors more diffuse because of lighter feather tips.

Measurements (in millimeters).—Breeding males (97 specimens): wing, 97.3 (102.1–91.1); tail, 64.7 (71.1–60.3); bill from nostril, 9.0 (10.3–8.1); tarsus, 20.4 (22.0–17.7); middle toe without claw, 10.0 (11.7–9.0).

Breeding females (32 specimens): wing, 90.9 (95.7–85.3); tail, 58.3 (62.0–53.0); bill from nostril, 8.4 (9.1–8.0); tarsus, 19.8 (21.5–18.0); middle toe without claw, 9.6 (10.6–8.9).

Distribution.—Resident throughout coast-range area of California from Capetown, Humboldt County, south to about latitude 30 degrees, in northern Lower California; south of there intergrading with *enertera*. Also occupies the central part of the San Joaquin Valley of California, intergrading with *rubea* toward southern Sacramento Valley and blending into *ammophila* in extreme southern part of San Joaquin Valley.

Specimens examined.—This race has been more adequately represented than any other; 543 skins have been examined. Of these, 175 are breeding males, 76 breeding females, 149 autumn and winter males, 121 autumn and winter females, and 22 juveniles. Localities which these specimens represent follow. Breeding localities are indicated by an asterisk. Unless otherwise stated the specimens are in the Museum of Vertebrate Zoölogy.

CALIFORNIA.—Humboldt County: Divide between Bear and Eel rivers, 7 mi. from Capetown*, 4. Sonoma County: Cotati*, 4 (Mailliard coll.); Petaluma*, 2 (Dickey coll.); 1 (Mus. Vert. Zoöl.). Marin County: Miller, 2; Nicasio*, 1 (Mailliard coll.). Contra Costa County: 4 mi. E Tassajara*, 1; 1 mi. E Giant*, 1; Moraga Valley*, 9 (McLean coll.); ½ mi. S Byron Hot Springs*, 33. Alameda County: El Cerrito*, 2 (McLean coll.); Newark*, 1 (Mailliard coll.); Berkeley*, 1; Oakland*, 2; Melrose, 5; Bay Farm Island, 1; Livermore*, 1; Hayward*, 4 (Mailliard coll.). San Francisco County: Merced Lake*, 2. San Mateo County: South San Francisco*, 3. Santa Clara County: Palo Alto*, 7. Santa Cruz County: Santa Cruz*, 1. San Benito County: 5 mi. SE Gilroy, 1 (McLean coll.); near Dixon Springs, 1900 feet, 8 mi. NW New Idria*, 8; Panoche Creek, 1200 feet, 2 mi. SE Panoche*, 11. Monterey County: Pacific Grove*, 2 (Mus. Vert. Zoöl.), 1 (Dickey coll.); San Lucas, 1; 4 mi. SW Gonzales, 4 (McLean coll.). San Luis Obispo County: Cuyama Valley*, 1; Morro, 10. Santa Barbara County: Santa Barbara*, 2 (Santa Barbara Mus.), 1 (Dickey coll.); Goleta, 8 (Dickey coll.); 4 mi. SW Goleta*, 4 (Santa Barbara Mus.). San Joaquin County: Stockton, 10; Tracy*, 2; La Grange, 10; 15 mi. SE Oakdale*, 6 (Law coll.); Pleasant Valley, 3. Merced County: Los Baños, 8; Snelling, 3; 10 mi. SE Turlock, 7; 1 mi. S Merced Falls*, 1; Planada, 4. Madera County: Chowchilla*, 5 (Mailliard coll.). Fresno County: Hayes Station, 19 mi. SW Mendota*, 2; 2 mi. SW Friant*, 4; Burrell*, 1 (Law coll.); 6 mi. E Panoche, 2 (McLean coll.). Tulare County: Tipton*, 2; Earlimart*, 9. Kings County: Corcoran, 1 (Dickey coll.). Kern County: "plateau land," San Emigdio Creek, 1600 feet, 1; Buena Vista Lake, 7 (Dickey coll.); 7 mi. SW Tehachapi, 2 (McLean coll.). Ventura County: Oxnard, 4 (Dickey coll.); Ventura*, 7; Cuddy Canyon, 4400 feet, Frazier Mountain*, 2; Mt. Pinos*, 1 (Dickey coll.). Los Angeles County: Highland Park, 5; Pomona*, 1 (Law coll.); Claremont*, 1 (Dickey coll.); Pasadena, 33; El Monte, 4; Long Beach*, 4 (Mus. Vert. Zoöl.), 8 (Dickey coll.); Wilmington, 1 (Dickey coll.); Palms, 3 (Dickey coll.). Orange County: Huntington Beach*, 1 (Law coll.); Newport*, 1 (Law coll.). San Bernardino County: Baldy Mesa Landing Field, El Cajon Pass*, 1 (McLean coll.); George Jr. Republic, Puente Hills*, 1; vicinity Colton*, 18; Oro Grande, 1 (Dickey coll.); Doble, 7000 feet, San Bernardino Mountains, 7; Big Bear Valley, San Bernardino Mountains*, 2 (Dickey coll.); San Gorgonio Peak, 11,485 feet, San Bernardino Mountains, 1; Chino*, 3 (Dickey coll.). Riverside County: Banning*, 1; Kenworthy *, 5; San Jacinto Lake, 1 (Dickey coll.); Corona, 2 (Law coll.); 10 mi. S Ontario, 2 (Dickey coll.); Mecca, 1; Thermal, 2 (Dickey coll.); Beaumont, 2 (Dickey coll.); Riverside, 19. San Diego County: Warners Ranch, 2 (Dickey coll.); Hilldale, vicinity of El Cajon, 3 (Dickey coll.); Julian*, 1;

Montezuma Valley*, 1 (McLean coll.); Pamo Valley, north of Ramona, 1 (McLean coll.); La Presa, 23; 1 mi. W Santee, 4; vicinity of San Diego*, 9; Chula Vista*, 1 (McLean coll.); Imperial Beach, 2 (Law coll.); Point Loma, 1; National City, 1 (Dickey coll.); Jacumba*, 36 (Dickey coll.), 17 (Law coll.).

LOWER CALIFORNIA.—West coast, 5 mi. S monument 258 at United States boundary, 10; Las Palmas Canyon, 15 mi. S north end Lower California, 1; El Valle de la Trinidad, 2500 feet, 7; Soccoro, 4; 4 to 6 mi. W San José, 2800 feet, 10; Santo Domingo, 4; San Telmo, 600 feet*, 2; San Ramón, at mouth of Santo Domingo River*, 11.

Habitat notes.—This race is outstanding in its range of ecological tolerance. Unlike some races already discussed, I know of no habitat features peculiar to it alone. In the extreme northern part of its range it occurs in open areas in a generally timbered country. The same is true, more or less, in the high mountains of the southern parts of the range. Horned larks of this race occur in the usual types of places, such as stubble fields, alkali flats, sea plains along the ocean front, roadways, and, in mountain regions, on valley floors sparsely covered with vegetation. They are especially abundant in the San Joaquin Valley, on low, level or rolling, open, pastureland. The range of altitude during the breeding season is from sea level to 8500 feet. Nor, apparently, are these birds limited in distribution by factors of temperature or humidity, being found in areas of slight humidity and of only a few inches of rainfall per year, but also in other regions of relatively high humidity and 30 or more inches of rainfall.

Distribution and variation.—The race *actia* presents many hindrances to exact expression of geographic variation by means of our current system of nomenclature. There seems to be more variation in color among specimens from the range of *actia* than has been encountered in any other race. Here is a situation that requires the tact, moderation, and knowledge of which Stresemann (1936:158) speaks, when he states: "It is not the task of *nomenclature* to express all systematic judgment, it must suffice that it expresses the *essential* part of it, and we should always be careful not to overdo." The facts of variation in horned larks in the range assigned to *actia* would not, in my opinion, be presented more clearly if the present race were split up further. To subdivide it would result in utter confusion. However, the details of local variation and trends of variation must not go unmentioned.

The race *actia,* as here delimited, comes into actual contact on its borders with five other races, with each of which it intergrades in one respect or another. First, with reference to *leucansiptila,* we find no evidence of blending of the two races over a long geographic gradient. In southern California, the coast range has at its east base a long and abrupt escarpment, which in the Salton Sea area forms the western boundary of the Colorado Desert. This physical feature, together with accompanying differences in climatic conditions, apparently serves to separate the two races. Yet the separation is not absolute for there are certain intermediate specimens and also more or less typical individuals of one race taken within the normal range of the other.

On April 21, 1934, in Pamo Valley, north of Ramona, San Diego County, Mr. Donald D. McLean and Mr. Gordon True noted a pair of horned larks

carrying on mating activities. The male of the pair was conspicuous because of its paler, lighter coloring. It was this that served to attract their attention to it. The male, upon collection (now no. 1136 in the McLean collection), proved to be fairly typical of *leucansiptila*. Nearby another pair was observed at about the same time. The male of this second pair was also obtained (now no. 1137, McLean collection) and proved to be typical of the race *actia*. All other horned larks observed in the upland area were dark like *actia*. This example serves to show that members of the lowland race do occasionally range up into the higher country and may interbreed with the resident race *actia*. The offspring of such interracial crosses we would expect to be intermediate in their characters between the two races. That this is probably true is indicated by one other male (no. 1138, McLean collection) taken in Montezuma Valley, San Diego County, at a locality near the upper edge of the escarpment. This specimen is intermediate between *actia* and *leucansiptila*.

That the reverse situation occurs, wherein members of *actia* move down and interbreed along the edge of the range of *leucansiptila*, is indicated by certain intermediates in the lowland area which seem closest to *actia*. As additional evidence of racial crossing, we have in the Dickey collection two examples of *leucansiptila* taken March 17, 1921, at Jacumba, San Diego County, the type locality of *actia*. These may not have been breeding birds, yet there is the possibility that they were stragglers that might thus have stayed to interbreed with the resident race.

Admittedly this is fragmentary evidence, but I do not think we should underestimate the role of racial hybridization on the borders of races. It is doubtless a phenomenon of widespread occurrence. It is more readily apparent in the present instance because examples of the two races are so distinct and because the physical features involved serve to bring it to our attention.

Intergradation of *actia* with *ammophila* is somewhat comparable in places to that with *leucansiptila*, although the effects are not so clear because the former two races are distinguished on such slight basis. In general, it may be said that mountain ranges separate these two races. Occasionally, however, these physical barriers break down and we find areas of intergradation. In just one instance is there evidence of the gradient type of intergradation of *actia* with *ammophila* and that is in the southern San Joaquin Valley. This will be discussed in my account of the latter subspecies.

Intergradation with *enertera* occurs in the form of a long gradient. Along the Pacific side of Lower California from about latitude 30 degrees (San Agustín) southward to latitude 29 degrees (Playa María) specimens become progressively paler. This trend culminates in a pale center of differentiation expressed by the name *enertera*. This is discussed in more detail in the account of that race.

With *rubea* also, we find a gradient of intergradation in the upper San Joaquin Valley, extending north into the lower Sacramento Valley. This is one of the most conspicuous examples encountered of this type of intergradation; and the decision where one race begins and the other ends is purely an arbitrary matter.

Actia intergrades with *insularis* by individual variation, as we have seen. The possibility has also been discussed that *insularis* may breed on the mainland. There is to date no evidence that *actia* meets or intergrades with *strigata*. Because of the broken and heavily timbered country between the northernmost record-station of *actia* and the southernmost occurrence of *strigata*, and because of the vast distance between, I am in doubt whether there is any contact at all between breeding populations of these two races. Neither does *actia*, so far as I know, come into direct contact with *sierrae*.

Difficulties in working out the variation and distribution of *actia* are thus encountered in connection with the intergradation with neighboring races. Also, there is an extreme amount of individual variation present in large series from any one place. But even more confusing is the intraracial geographic variation. This is best elaborated, perhaps, by discussing regional differences in specimens taken within the range designated for the race as a whole.

Regional differences.—Northern coast region: Specimens from the east San Francisco Bay region, particularly those from El Cerrito in Contra Costa County and north to Bay Point in the vicinity of the Carquinez Strait, are intergrades between *actia* and *rubea,* as is shown by the increased amount of ruddy on the head and nape. This *rubea* influence seems to extend even as far south as the southern end of San Francisco Bay, judging by certain specimens from Palo Alto, which are so extremely ruddy that they show a remarkable resemblance to *rubea.* Specimens from the Suisun Bay region and north and east of it I have referred to *rubea,* but in Marin County, on the west side of San Francisco Bay, good *actia* is found. Specimens are few from this last-named area, but those present from Miller and Cotati, Marin County, and from Petaluma, Sonoma County, are fairly typical of *actia.*

Horned larks occur up the coast sporadically in Sonoma and Mendocino counties. The only representatives at hand from the coastal section north of Marin County, however, are three July males and a juvenile from Humboldt County, taken 7 miles east of Capetown, on the divide between the Bear and Eel rivers. Grinnell (1931:74) has recorded these as *strigata,* and on this basis the race was given breeding status in California. In my opinion these specimens are referable instead to *actia.* It is true that on the basis of habitat alone these would appear to be *strigata;* they come from the humid coast belt of northern California and *strigata* is confined almost exclusively to that type of habitat in the Pacific Northwest. However, the males are characterized by solid ruddy on the head and nape and entirely lack any vestige of dark feather-centers and the dark brown back of *strigata,* as well as the yellow below. Their average size is close to that of *strigata* from the Puget Sound region; but it is to be recalled that the geographically nearest examples of *strigata,* representing the southernmost outpost of that race, from Medford, Jackson County, Oregon, average considerably larger than the Puget Sound examples. Therefore, the southernmost examples of *strigata* are not comparable to the Capetown examples in measurements.

In the solid ruddiness of head and nape, which also extends part way down

the back, these Capetown specimens resemble somewhat the condition in *rubea,* but this condition can be perfectly matched by specimens of "good" *actia* from as far south as Ventura. The Capetown birds are separated from *rubea* of the Sacramento Valley by the width of the coast ranges, an area apparently free of horned larks. Even though there are some few suitable places in these ranges where such birds might exist, they do not seem to have pushed in there. I failed to find them in the spring of 1933 on the Bald Hills in Humboldt and Trinity counties, localities which seemed entirely suitable for them. It may be that along the coastal strip, *actia* runs still farther north and meets true *strigata,* but I rather doubt it, considering the rough and timbered nature of the country. It seems likely, then, that these two races probably do not intergrade.

Southern coastal area: Specimens from Pacific Grove and south along the coast to southern California are conspicuously ruddy brown on their backs and are more heavily pigmented than specimens from the interior.

Breeding specimens from Ventura are very ruddy on the head and nape; in many this ruddy extends so far down on the back that a remarkable resemblance to *rubea* is produced. To the south, specimens from Pasadena and even from San Diego continue to show this ruddy on the nape, but in addition warm brown appears elsewhere on the dorsal surface, serving to characterize birds from this region. Although it is doubtful whether one should, under the circumstances, try to designate subspecifically typical representatives of this race, I would say that it is from the Los Angeles–San Diego region that one finds the most characteristic examples of *actia.* In making this assertion, it is well to call attention to the high incidence of adventitious coloring that appears in birds from this region, apparently caused by the reddish soil. This is especially noticeable in series from Chula Vista and Santee, San Diego County.

Northern Lower California: The race *actia* extends southward in Lower California on the Pacific slope to about latitude 29 degrees. It also occurs, in winter at least, on islands near the coast. In the vicinity of latitude 29 degrees there are evidences of intergradation with *O. a. enertera* which will be presented under that race.

Actia is the form found in the high meadows of the Sierra San Pedro Mártir. Grinnell (1928:16), in discussing differentiation areas, refers particularly to the peculiar climatic area in this San Pedro Mártir region of northern Lower California. He stated: "Here, between the crest of the Sierra San Pedro Mártir and the Pacific, is what may be termed a *humid desert;* that is to say, there exists a region of meager rainfall but of high atmospheric humidity. Fog or cloudiness is frequent over an intensely dry terrane! The notable thing is that this combination of conditions brings similar modifications (deepened coloration, certain proportions of wing and tail, lesser size of bill, etc.) in various birds which are very remotely related to one another phylogenetically." Anthony (1893:238) recorded specimens from the San Pedro Mártir and remarked that they were markedly dark in color. December specimens in the Museum of Vertebrate Zoölogy from six miles west of San José, 2800 feet, Lower California, are also darker than most representatives of *actia.*

There is ample evidence, therefore, of a local darkening of dorsal color tone in northern Lower California. The exact northward extent of this local variation is not entirely known. In the topotypical series of *actia* taken in August at Jacumba, there are certain abnormally dark examples, already mentioned in connection with *insularis*, which, if worn a little, would resemble the San Pedro Mártir birds. This would indicate that the trend leading to this local intensification of color starts as far north as the international boundary.

Lower San Joaquin Valley: As indicated in our discussion of *rubea*, it is purely an arbitrary matter where to draw the line separating *rubea* and *actia*. The one race blends directly but gradually into the other over a hundred-mile sweep. From the center of differentiation of *rubea* in the vicinity of Red Bluff and Oroville, the transition occurs southward through the lower Sacramento Valley into the San Joaquin. The increased ruddy on specimens, particularly on the nape, is to be seen on examples as far to the south as Fresno. South of here a paling occurs as *ammophila* is approached in the Buena Vista Lake region. One striking instance of parallelism is the resemblance of specimens from Oakdale and vicinity, Stanislaus County, to those from Ventura, Ventura County.

Variation among juveniles.—The juveniles of *actia* are as a whole darker than those of the closely related race *ammophila*. But among the representatives of *actia* an almost incredible range of variation is to be seen. Quite the darkest juvenile is one from near Capetown in Humboldt County. It is characterized by an increased amount of blackish on the back, causing it to resemble a juvenile of the race *merrilli* from Likely, Modoc County, California. A specimen from the southern part of the range of *actia* at San Jacinto Lake, Riverside County, is also deeply pigmented. It resembles the northern specimen closely except that it is browner, less blackish. Another deeply pigmented specimen is from Pacific Grove, Monterey County. However, this one is distinctive by way of its reddish brown color. It shows a closer resemblance to juveniles of the race *rubea* and to juveniles from the area of intergradation between *rubea* and *actia* at Byron, Contra Costa County, than it does to other representatives of the race *actia*.

The outstanding example of purely individual variation encountered among juveniles of any race of horned lark concerns a series of four individuals from Earlimart, Tulare County. These specimens were taken May 1 and 3, 1911. The differences cannot be attributed to sexual variation because opposite extremes occur in the same sex. Number 19489, female, is of a decided warm brown color. On the other hand, no. 19490, also a female, is grayish black, hence totally unlike the former one. The other two, both males, are more alike, nearer brown than black, but intermediate between the two extremes mentioned. The fact that Earlimart is on the periphery of the range of *actia* and near where *ammophila* comes in, may indicate the reason for this increased amount of variability. Other representatives of *actia* from Los Baños, Merced County, Claremont, Los Angeles County, and Mount Pinos, Ventura County, are uniform in their coloration, but lighter than the deeply pigmented specimens already described.

Just as adults of *actia* show more individual and geographic variation than is found in other races, so do the juveniles. It is not unreasonable to believe that juveniles so different would develop into adults showing equally great differences. There seems to be no alternative except to recognize this as extreme individual variation.

Summarizing conditions in the range of *actia,* we may say in general that specimens from the coastal strip are browner than those from interior regions. In the Great Valley of California the trend southward is from ruddy to paleness; this is duplicated as one goes southward coastwise in northern Lower California. The same tendency is observed moving westward in southern California from the coast toward the Mohave and Colorado deserts. In connection with these trends there is often intergradation with other races, which probably accounts in part for the great amount of variability presented. It also should be kept in mind that horned larks from the range of *actia* are resident the year round and thus are more subject to the local environmental influences than are migratory races. Also, this race has a widespread range in which a great many kinds of environmental situations are encountered. Where there are no physical barriers, we find far-flung integradation, as in the San Joaquin Valley; where such barriers are present, the intergradation is of an irregular type and of limited occurrence.

Otocoris alpestris ammophila Oberholser

Mohave Horned Lark

Otocoris alpestris arenicola, Dwight (1890:146), part; Fisher (1893:66), part; Bendire (1895:338); Grinnell (1902:44)

Otocoris alpestris chrysolaema, Fisher (1893:67), part

Otocoris alpestris pallida, Lamb (1912:37)

Otocoris alpestris ammophila Oberholser (1902:849), original description; Ridgway (1907:321); Grinnell (1912:15); Grinnell (1915:95); Dickey and van Rossem (1922:68); Dawson (1923:841); Grinnell (1932:287); Linsdale (1936:80); van Rossem (1936a:32)

Chionophilos alpestris ammophilus, Hellmayr (1935:8)

Type.—Adult male, no. 139892, U. S. Nat. Mus., near Maturango Spring, Coso Valley, Inyo County, California, May 11, 1891, collected by T. S. Palmer.

Diagnosis.—In coloration, midway between *actia* and *leucansiptila,* being lighter than *actia* and darker than *leucansiptila;* comparable in size to these two races; smaller than *lamprochroma* and with warmer brown, less grayish, and less contrast between nape and back; differs likewise from *utahensis,* showing no trace of ashy coloration.

Measurements (in millimeters).—Breeding males (77 specimens): wing, 98.9 (103.4–95.4); tail, 65.8 (70.2–60.1); bill from nostril, 9.3 (10.5–8.3); tarsus, 20.6 (22.0–19.4); middle toe without claw, 10.2 (11.6–8.3).

Breeding females (27 specimens): wing, 92.1 (96.1–88.8); tail, 58.7 (63.8–54.8); bill from nostril, 8.5 (9.1–7.7); tarsus, 19.8 (21.1–18.9); middle toe without claw, 9.9 (10.8–9.2).

Distribution.—Resident in the Mohave and Amargosa deserts of southeastern California and southwestern Nevada; also in the extreme southern San Joaquin Valley of central California.

Specimens examined.—Representatives of this race examined total 242 skins. Of these, 101 are breeding males, 45 breeding females, 67 autumn and winter males, 22 autumn and winter females, and 7 juveniles. Skins are from the following localities. Unless otherwise

indicated, specimens are in the Museum of Vertebrate Zoölogy. Breeding stations are indicated with an asterisk.

CALIFORNIA. Inyo County: Olancha, 1; Keeler*, 6; Kelley's Well, Amargosa River*, 2; Emigrant Canyon, 4899 feet, Panamint Mountains*, 6; 4 mi. SSE Junction Ranch, 5700 feet, Argus Mountains, 5; Lee Flat, 15 mi. N Darwin, 1. Kern County: Mohave, and 1 mi. W Mohave*, 13; Los Angeles Aqueduct, 3100 feet, 5 mi. W Mohave, 4; southwest part of Walker Basin, 17; Rankin Ranch, Walker Basin, 2; Kelso Creek, 2 mi. N Sageland, 3; Monolith, 3; 2 mi. N Edison Station*, 3; Tehachapi*, 2; Weldon*, 3; Onyx*, 1; Kern River at Bodfish*, 2; "plateau land," San Emigdio Creek, 1650 feet*, 1; Buena Vista Lake*, 35 (Dickey coll.). Tulare County: Monache Meadow, 8000 feet, 1. San Luis Obispo County: Simmler*, 6; 1 mi. W Simmler*, 1; 7 mi. SE Simmler, Carrizo Plains*, 1. Los Angeles County: Fairmont, Antelope Valley*, 7; 1½ mi. W Fairmont, 2; Lancaster, 1; Palmdale*, 10 (Dickey coll.), 21 (Mailliard coll.); 5 mi. E Palmdale*, 15 (Dickey coll.); San Fernando Valley*, 3. San Bernardino County: Victorville*, 19 (Dickey coll.), 5 (Mus. Vert. Zoöl.); Hesperia*, 11 (Dickey coll.), 6 (Mus. Vert. Zoöl.); Oro Grande, 2 (Dickey coll.), 8 (Mus. Vert. Zoöl.); Newberry Springs, 1 (Dickey coll.); Ludlow*, 2. Imperial County: 20 mi. E Holtville, 2 (Dickey coll.); Kane Spring, 2 (Dickey coll.); south shore Salton Sea, 1 (Dickey coll.).

NEVADA. Nye County: 19½ mi. SE Goldfield*, 1. Clark County: Smith Ranch, 6000 feet, Charleston Mountains, 4 (Dickey coll.).

Habitat notes.—The range of *ammophila* coincides fairly closely with the Mohave Desert. The climate is a typical desert one, with low humidity, little rainfall, high summer temperatures, the maxima ranging from 90 degrees to 130 degrees Fahrenheit, and low winter temperatures averaging from 15 degrees to 50 degrees (Jepson, 1925:4). There is, then, a great annual range of temperature as well as a great diurnal range. The altitudinal range of the floor of the Mohave Desert is from 2000 to 5000 feet. The gray-hued shrubs of the desert are widely spaced. Creosote bush (*Larrea tridentata*) is common over hundreds of square miles in the range of *ammophila*. Species of *Atriplex* are common, as are burro-weed (*Franseria dumosa*), desert thorn (*Lycium* sp.), and sea blite (*Suaeda suffrutescens*), the latter characteristic of the margins of alkaline valleys, where horned larks may be found.

Distribution and variation.—When Oberholser diagnosed *ammophila* he stated (1902:850) that it could easily be distinguished from *actia* by its very much paler color above. Ridgway (1907:321) found *ammophila* similar to *actia* but slightly larger and with upper parts much paler. The race has been generally accepted down through the years, though certain systematists probably have had mental reservations with respect to the separability of *actia* and *ammophila*. Some have been inclined to attribute the differences between representatives of the two races to a differential rate of feather wear and abrasion. There is no doubt that this factor is an important consideration, but the fact remains that there are actual differences, though slight, to be seen in series of birds in fresh fall plumage from within the ranges of the two races. Examination of such material shows that birds from the ascribed range of *ammophila* average slightly paler than representatives of *actia*. The feather edgings particularly are lighter, producing a general tan color, of lighter tone than in *actia*. Breeding birds show a greater degree of difference because of greater feather deterioration in the more arid desert region.

There arises, then, the question whether these differences are of sufficient intensity to justify recognition of the Mohave birds as a separate race; here the personal equation enters. From my own study, I believe the amount of differentiation shown is as great as that which exists between many western races of geographically variable birds and that there is uniformity of characters in *ammophila* equal to that in many races. If I should refuse to recognize *ammophila*, then to be at all consistent I would also have to throw out several other "weakly" differentiated races of horned larks. Since there is evidence of yet further differentiation within the range of this race, just as within those of others that are likewise weakly characterized, the actual situation is better indicated by the retention of *ammophila* than it would be, were *ammophila* lumped with *actia*. As will be emphasized later, there are all degrees of sub-specific divergence.

Part of the difficulty in distinguishing between *actia* and *ammophila* arises from the fact that there are few specimens available from the area where *ammophila* appears to develop in extreme degree. This area seems to extend from Owens Lake east to the Amargosa Desert and south to the vicinity of Ludlow, San Bernardino County, California. Examples from this specified area are readily distinguishable from representatives of *actia*. On the other hand, *ammophila* blends gradually into *actia* westward from the central Mohave Desert, as also northward through the Tehachapi Mountains into the southern San Joaquin Valley. Breeding examples from these broad regions of intergradation are abundant in collections. Since they have been considered by many as typical of the Mohave Desert race, it is little wonder that skepticism has arisen concerning the tenability of the name *ammophila*.

The palest specimens at hand from the range of *ammophila* are from Keeler, Inyo County, California. This is true both for breeding birds and for examples in fresh fall plumage. These specimens are, however, somewhat larger than those from elsewhere in the range and in this respect seem to foreshadow an approach to *lamprochroma* to the north. Indeed, a little farther north of the area whence typical specimens of *ammophila* come, one finds definite evidence of intergradation with *lamprochroma*. This blending of the two races occurs from Benton, Mono County, north into west-central Nevada. Autumn-taken birds from Oasis, Mono County, California, and from Deep Springs Valley are intermediate in color between *lamprochroma* and *ammophila,* being closer, perhaps, to the former. Breeding examples from Arlemont, Esmeralda County, Nevada, also show an approach to *ammophila*. Thus the transition between these two races occurs over a long stretch in the northern part of Owens Valley and in the country to the east from Fish Lake Valley south through Deep Springs Valley.

There is still no evidence that horned larks occur in Death Valley during the breeding season, although individuals have been taken there in the autumn. From the area to the east of Death Valley, a pair of breeding birds, clearly of the race *ammophila,* is present from Kelley's Well on the Amargosa River.

The four birds taken by van Rossem (1936a:32) in the Charleston Mountains in southeastern Nevada are badly worn and little can be judged from

their color, but they seem closest to the Mohave race. The specimen from 19½ miles southeast of Goldfield, Nye County, Nevada, designated as *ammophila* by Linsdale (1936:80), seems closest to this race and therefore is the northernmost specimen of "good" *ammophila* known.

The southeasternmost breeding representatives of this race are from Ludlow, San Bernardino County. Two males from there are light-colored and show no approach to *leucansiptila*. This is suggestive of a rather sudden transition from one race to the other south of this point. The ranges of these two races thus seem to conform fairly well to the extent, respectively, of the Mohave and Colorado deserts as usually mapped.

Series of breeding birds from Hesperia and Victorville in eastern San Bernardino County and from Palmdale, Los Angeles County, California, show the essential characters of *ammophila* but are less distinct from *actia* than are those examples mentioned from farther east. The series shows, however, considerable individual variation. All the localities mentioned are on the Mohave Desert north or east of the prominent mountain ranges that form its western and southwestern boundaries. Since the horned larks in the mountainous country west and southwest of these localities are referable to *actia,* it appears that *ammophila* is confined to the desert proper in this area and that, in general, these coast ranges furnish a natural boundary between *actia* and *ammophila.*

One exception to this statement concerns breeding birds taken in the San Fernando Valley, Los Angeles County. Three males collected there in April are lighter in color than are examples of *actia* and hence seem closest to *ammophila*. This valley is on the coastal side of the mountains but is, nevertheless, dry and hot. It supports a type of vegetation that contains certain elements typical of the Mohave Desert. Since the horned larks in this valley seem thus to be of Mohave Desert extraction, the mountains have probably not proved to be an insurmountable barrier. Access to the valley from the desert is possible over passes at the headwaters of the Santa Clara River.

In the northwestern part of the range of *ammophila,* a number of minor complications in distribution arise, together with some puzzling local variation. Several breeding birds from one mile south of Mohave are darker brown than are the Palmdale, Victorville, or Hesperia examples. They suggest an approach to *actia,* but they are close to the center of the range of *ammophila.* Even a fall bird from fifteen miles north of Darwin is considerably darker than other fall representatives of the race. This local darkening in the midst of an area of general paleness is difficult to explain, except as the result of extreme individual variation.

Another anomalous situation concerns the breeding birds of the Buena Vista Lake region in Kern County at the southern end of the San Joaquin Valley. This is north of the Tehachapi Range, which separates the San Joaquin Valley from the Mohave Desert. Both breeding and autumn horned larks from near Buena Vista Lake are paler than the breeding birds to the north and to the west. They are thus perhaps best referable to *ammophila,* as first pointed out by Dickey and van Rossem (1922:68). If their affinities are really with

this race, the Tehachapi Mountains do not act as a formidable barrier. In fact, these mountains are so low that horned larks undoubtedly breed where fields exist along their crests, as is indicated by a breeding male from Tehachapi. In this connection, it should be emphasized that the southern end of the San Joaquin Valley, especially on its west side, is very arid, being in places more of an absolute desert than most of the Mohave Desert itself. We find here a quite different habitat from that existing within the range of *actia*.

Breeding horned larks from the Carrizo Plains, San Luis Obispo County, although showing an approach to *actia,* are pale and best referable to *ammophila*. The hypothesis of their close relationship to *ammophila* is strengthened by the presence of a juvenile from seven miles southeast of Simmler, San Luis Obispo County, that is notably paler than juveniles of *actia* and entirely comparable with juveniles of *ammophila*. North of Buena Vista Lake, specimens from the Tulare Basin, as around Corcoran, Kings County, are much darker brown and hence of the race *actia*. There is, as has been previously pointed out, a trend from there northward toward *rubea,* or, in other words, a gradual intensification of ruddy coloring. Although the specimens in this intermediate region are most like examples of *actia* elsewhere, the possibility occurs to me that they may be intergrades between *ammophila* and *rubea* which thus happen to resemble *actia*.

Fall representatives from the Walker Basin, from Kelso Creek, 2 miles north of Sageland, and from Monolith, Kern County, are all of the *ammophila* type. Mixed with the specimens of *ammophila* from the Walker Basin are many October-taken examples of *utahensis* which are evidently migrants from the Great Basin. During the breeding season, representatives of *ammophila* probably occur in isolated colonies throughout this whole area.

One particularly important specimen is a female of the year taken August 5, 1911, at Monache Meadows, 8000 feet, Tulare County, California. This represents the northernmost locality in the southern Sierra Nevada from which specimens are at hand. This specimen, no. 20035 Mus. Vert. Zoöl., is in molt. Most of the dorsal feathers are new, but around the head and neck many juvenal feathers still remain. Having been taken so early in the fall it was, in all probability, raised in the immediate vicinity. According to the collector's notes, many others were observed at the same time but only this one was obtained. This specimen is not *lamprochroma* or *sierrae,* nor is it suggestive of another race in the southern Sierra Nevada. Its characters leave no doubt in my mind that it is of the race *ammophila*. The new back feathers have very pale edgings. If all the new feathers were present, the mass effect would be as light as in the fall specimens of *ammophila* from Walker Basin. Equally indicative is the pallor of the remaining juvenal feathers.

In the Mount Pinos region of Ventura County occur what appear to be intermediates between *actia* and *ammophila*. Specimens from Cuyama Valley, San Luis Obispo County, Cuddy Canyon, 4400 feet, Frazier Mountain, Ventura County, and Cuddy Valley, Kern County, are closest to *actia* but show an approach to *ammophila*. However, a breeding male from San Emigdio Creek, 1650 feet, Kern County, is referable to *ammophila,* though not typical.

There seems to be about the average amount of individual variation in dorsal color in some of the breeding series representative of this race. Occasionally specimens are encountered which have a scorched appearance dorsally; in this they resemble members of the race *adusta*, in which this character is fixed and constant. The character is not of an adventitious nature in these few individuals, for it appears both in breeding and fresh-plumaged birds and in birds from widely separated areas. Breeding specimens showing this feature are among the series from Buena Vista Lake, Palmdale, and Victorville. Fall examples that are so distinguished also occur in these series and in that from Junction Ranch, Argus Mountains. The significance of this in a race that is for the most part resident and apparently widely separated from *adusta* is not clear. It may be indicative of great heterozygosity.

Occasionally, among breeding series of *ammophila* there are found darker-backed specimens suggestive of *actia*. Most of these individuals have lighter napes and thus indicate a degree of morphological intermediacy. In general, then, it seems that there are a great many aberrants in *ammophila* populations that are not geographically intermediates; whether they are intermediates by way of individual variation, or whether they are wanderers from other areas, cannot be determined with certainty.

Otocoris alpestris leucansiptila Oberholser

Sonora Horned Lark

Otocoris alpestris pallida (Townsend MS) Dwight (1890:154), original description; Townsend (1890:138); Bendire (1895:374); Oberholser (1902:863); Ridgway (1907:326); Swarth (1914:44)

Otocoris alpestris leucansiptila Oberholser (1902:864), original description; Ridgway (1907:327); Grinnell (1912:15); Grinnell (1915:95); Nelson (1921:126); Dawson (1923:842); Willett (1933:112)

Chionophilos alpestris dwighti Stresemann (1922:88), original description; Hellmayr (1935:9)

Chionophilos alpestris leucansiptilus, Hellmayr (1935:9)

Type.—Adult male, no. 132970, U. S. Nat. Mus.; Yuma, Yuma County, Arizona; March 13, 1894; collected by E. A. Mearns and F. X. Holzner.

Diagnosis.—More bleached and paler toned than either *actia* or *ammophila*, with upper surface more uniform and the nape more pinkish; slightly larger than either of the races named; less scorched or reddish brown than *adusta*; with more pale pink than *utahensis*, and smaller; closest in general pallor to *enertera*, but larger. *Leucansiptila* is the palest of all the North American races. Color of nape in typical specimens in fresh and relatively unworn plumages is Vinaceous-Fawn; back varies from Avellaneous to Wood Brown.

Measurements (in millimeters).—Breeding males (18 specimens): wing, 99.5 (101.7–97.3); tail, 67.4 (74.1–64.1); bill from nostril, 9.1 (9.9–8.2); tarsus, 20.7 (22.0–18.8); middle toe without claw, 9.8 (11.1–8.3).

Breeding females (11 specimens): wing, 93.5 (99.6–91.1); tail, 60.3 (63.1–56.8); bill from nostril, 8.6 (9.1–8.3); tarsus, 20.3 (21.1–19.8); middle toe without claw, 10.0 (11.1–9.6).

Distribution.—Resident in the Colorado Desert from extreme southwestern Nevada, southeastern California, and western Arizona to northeastern Lower California and extreme northwestern part of Sonora, Mexico.

Specimens examined.—The material assembled for this race totals 70 skins, of which 24 are breeding males, 15 breeding females, 25 autumn and winter males, 6 autumn and winter

females. No juveniles have been seen. The following stations are the places whence this material came. Unless otherwise indicated, the specimens are in the Museum of Vertebrate Zoology. Those localities designated with an asterisk are those from which breeding material has been examined.

NEVADA. Clark County: Arden, 1 (Dickey coll.).

ARIZONA. Yuma County: Harrisburg (Nord Ranch, 6 mi. S. Ehrenberg), 7.

CALIFORNIA. San Diego County: Pamo Valley, north of Ramona, 1 (McLean coll.); Jacumba, 2 (Dickey coll.). Riverside County: Moreno Valley, 1; Mecca^x, 19. Imperial County: Echo Island*, Salton Sea, 1; south end Salton Sea*, 2; 20 mi. E Holtville, 3 (Dickey coll.); Bard*, 1 (Dickey coll.); Fort Yuma, 1; Kane Spring*, 3 (Law coll.), 4 (Dickey coll.); 10 mi. W Kane Spring, 4 (Dickey coll.); Coyote Well*, 4.

LOWER CALIFORNIA. Alamo River, 20 mi. SE Pilot Knob, 11.

Habitat notes.—The range of *leucansiptila* coincides closely with the Colorado Desert, an area inclusive of clay and alluvial deposits of the Colorado River, old lake beds, sand hills, and alkaline flats. The range in altitude is from about 246 feet below sea level to 500 or more feet above. Lying, as it does, to the east of the abruptly rising mountain ranges which separate it from the coastal regions, this desert area has little precipitation, low humidity, and relatively high temperatures. The annual rainfall is less than five inches, and much of this occurs at rare intervals in "cloudbursts." Some years there are only traces of precipitation. Winds of gale force are of common occurrence. The temperature range is comparable to that given for the range of *ammophila*. *Leucansiptila* occurs abundantly in the cultivated areas of the Imperial Valley as well as in the truly desert sections.

Nomenclatural history.—In 1889, Charles H. Townsend collected a single male horned lark at Direction Hill, between Adair Bay and the mouth of the Rio Colorado, Sonora, Mexico. This seemed to belong to a different subspecies than any then known, so he described it in his report as *Otocoris alpestris pallida*. As happened with *insularis*, before Townsend's article appeared in print, Dwight's review of the horned larks was published; and in it Townsend's race was discussed under the name *pallida*. Actually, then, the first description of this supposed race was that given by Dwight; no type specimen was listed. However, in Townsend's article the type was definitely stated (1890:138) to be no. 117679, U. S. Nat. Mus., male, taken March 26, 1889, by C. H. Townsend near the mouth of the Rio Colorado, Sonora.

Oberholser (1902) considered this single specimen to represent a race different from that in the Colorado Valley; the latter he described as *Otocoris alpestris leucansiptila*. Consequently he assigned (1902:864) to *leucansiptila* a range in "extreme southwestern Arizona, extreme southeast corner of California, and northeastern Lower California along the international boundary line, north to southern Nevada." Concerning *pallida*, he stated (1902:864), "The type of *pallida*, which apparently represents the breeding birds of the region immediately about the head of the Gulf of California, at least on the eastern side, seems to be the only individual properly referable to this subspecies." Ridgway (1907:326) treated the situation in the same way. The A. O. U. Committee, in their 1910 check-list, treated *leucansiptila* as a synonym of *pallida*. Grinnell (1912:15) continued to employ the name *leucansiptila*,

but Swarth (1914:44) used the name *pallida* for the Colorado Valley race. Some years later, Stresemann (1922:88) discovered the name *pallida* to be preoccupied, and proposed in its place the name *dwighti*. Finally, Grinnell (1928:146), not convinced that there are two races in the Colorado Desert, restituted the name *leucansiptila*, synonymizing *dwighti* under this name. In this use of the name *leucansiptila* for the lower Colorado River valley race, he was followed by the A. O. U. Committee in its 1931 check list.

Thus the matter rests, at least until additional material is available from the northwest corner of Sonora. After observing the extremes in individual variation in horned larks, the broad areas of intergradation, the frequency of local differentiates, and the effects of wear and fading on feather coloration, I feel there is no justification for separating any race on the basis of a single specimen.

Distribution and variation.—*Leucansiptila* has the distinction of being one of the better-differentiated races of horned lark. Unlike some of the neighboring races, it seems to show little variation of a geographic nature. The specimens that show the characters best developed are from the Salton Sea region and Imperial Valley of California. Radially from this center there are indications of intergradation with two neighboring races, although insufficiency of material prevents detailed tracing of the trends.

Under our discussion of *actia*, it was noted that it and *leucansiptila* are separated more or less by natural barriers. Where these break down, as in the vicinity of San Gorgonio Pass, there may be a blending between the two races. Otherwise, the intergrading is sporadic, as the examples discussed below would indicate.

The San Gabriel–San Bernardino mountains project southeastward into the desert region of southeastern California between the ranges of *ammophila* and *leucansiptila*, thus confining *ammophila* to the Mohave Desert and *leucansiptila* to the Colorado Desert. All examples taken from these mountains are referable to *actia*. *Ammophila* and *leucansiptila* probably come together and intergrade yet farther to the southeastward; unfortunately, no material is at hand from this area. Practically nothing is known, either, of the transition, if such occurs, between *leucansiptila* and *adusta*.

In the northeastern part of the range of *leucansiptila* we find evidence of an approach to the race in the eastern part of the Great Basin. This is noticeable in a pair of skins in the Museum of Vertebrate Zoölogy from Penoyer Valley, Lincoln County, Nevada. These were taken on June 2, 1932, and are badly worn and faded. They are lighter and appear more bleached than *utahensis*. Also, the male has the nape region lighter, with this pallor extending far down the back, as occurs in examples of *leucansiptila*. A female in the Dickey collection taken in April in the vicinity of Arden, Clark County, Nevada, is also lighter than more northerly breeding examples. This trend toward *utahensis* takes place in the upper Colorado Valley and not through the Mohave Desert. This is indicated by the Ludlow, San Bernardino County, specimens, which are definitely referable to *ammophila*.

Oberholser (1902:865) discussed two winter specimens from Ash Meadows

in southern Nevada which seemed to him nearer *leucansiptila* than *ammophila*. He thought it probable that they would ultimately prove to represent the breeding horned lark of the area. That this is not so, however, is shown both by the specimens that van Rossem took at Smith Ranch, Charleston or Spring Mountains, Nevada, and the two from Kelley's Well, Inyo County, California. The last-named two, a breeding pair, taken April 1, now in the Museum of Vertebrate Zoölogy, although showing a slight approach to *leucansiptila*, seem to me closest to *ammophila*. The Smith Ranch examples were taken later, in July, and are consequently badly worn; but they, too, are closest to *ammophila*. *Leucansiptila*, then, apparently is confined to the valley of the Colorado River and does not invade the Mohave or Amargosa deserts. If it breeds in Nevada, it does so only in the extreme southern part of that state west of the Spring Mountains and along the Colorado River.

Otocoris alpestris enertera Oberholser

Magdalena Horned Lark

Otocorys alpestris chrysolaema, Belding (1883:530)
O[tocorys] alpestris rubeus Henshaw (1884:267) part
Otocoris alpestris chrysolaema, Bryant (1889:292)
Otocoris alpestris pallida, Dwight (1890:154), part; Bryant (1890:149)
Otocoris alpestris actia, Oberholser (1902:848), part; Ridgway (1907:320), part; Grinnell (1928:144), part
Otocoris alpestris enertera Oberholser (1907:41), original description; Ridgway (1907:890); Nelson (1921:126); Lamb (1927:70), part
Otocoris alpestris insularis, Lamb (1927:70)

Type.—Adult male, no. 196076, U. S. Nat. Mus.; Llano de Yrais (near Magdalena Bay), Lower California; December 13, 1905; collected by E. W. Nelson and E. A. Goldman.

Diagnosis.—Similar to *actia* but smaller and lighter in coloration throughout, particularly on nape and back; resembles *ammophila* and *leucansiptila* more closely in pallid coloration, but grayer and smaller than either. A January specimen at hand that is fairly typical is Army Brown on the back, with lighter feather edgings, while the nape is nearer Fawn Color.

Measurements (in millimeters).—Breeding males (22 specimens): wing, 96.5 (101.3–92.7); tail, 63.9 (69.1–58.0); bill from nostril, 9.5 (11.0–8.8); tarsus, 20.3 (21.7–18.8); middle toe without claw, 9.9 (11.0–9.0).

Breeding females (14 specimens): wing, 88.8 (92.2–87.0); tail, 56.8 (58.6–54.5); bill from nostril, 8.9 (10.3–8.0); tarsus, 19.6 (20.8–18.7); middle toe without claw 9.8 (10.4–9.2).

Distribution.—Resident in the west-central part of the peninsula of Lower California, from Santa Rosalía Bay region at about latitude 28 degrees, 40 minutes, south to the Magdalena Bay region at about latitude 24 degrees. Certain of the coastal islands are occupied, at least in summer.

Specimens examined.—Representatives of this race examined in connection with the present study total 71, including 22 breeding males, 16 breeding females, 15 autumn and winter males, 9 autumn and winter females, and 9 juveniles. These are from the following localities. Those marked with an asterisk are breeding localities. Unless otherwise indicated, specimens are in the Museum of Vertebrate Zoölogy.

Lower California. San Agustín, 12; Santa Rosalía Bay*, 4; San Benito Island*, 2 (Calif. Acad. Sci.); West San Benito Island*, 3 (Dickey coll.); Natividad Island, 10 (Dickey coll.); Turtle Bay*, 2 (Dickey coll.); San Jorge*, 3; Hiray, 75 ft., Llano de Hiray* [= Llano de Yrais], 30; Magdalena, Santa Magdalena Island*, 3; Almejas Bay, Santa Margarita Island*, 2.

Habitat notes.—Near Magdalena Bay, in the southern part of the range of the race, is Magdalena Plain. This, according to Nelson (1921), is the largest area of nearly level land on the peninsula except that composing the Vizcaíno
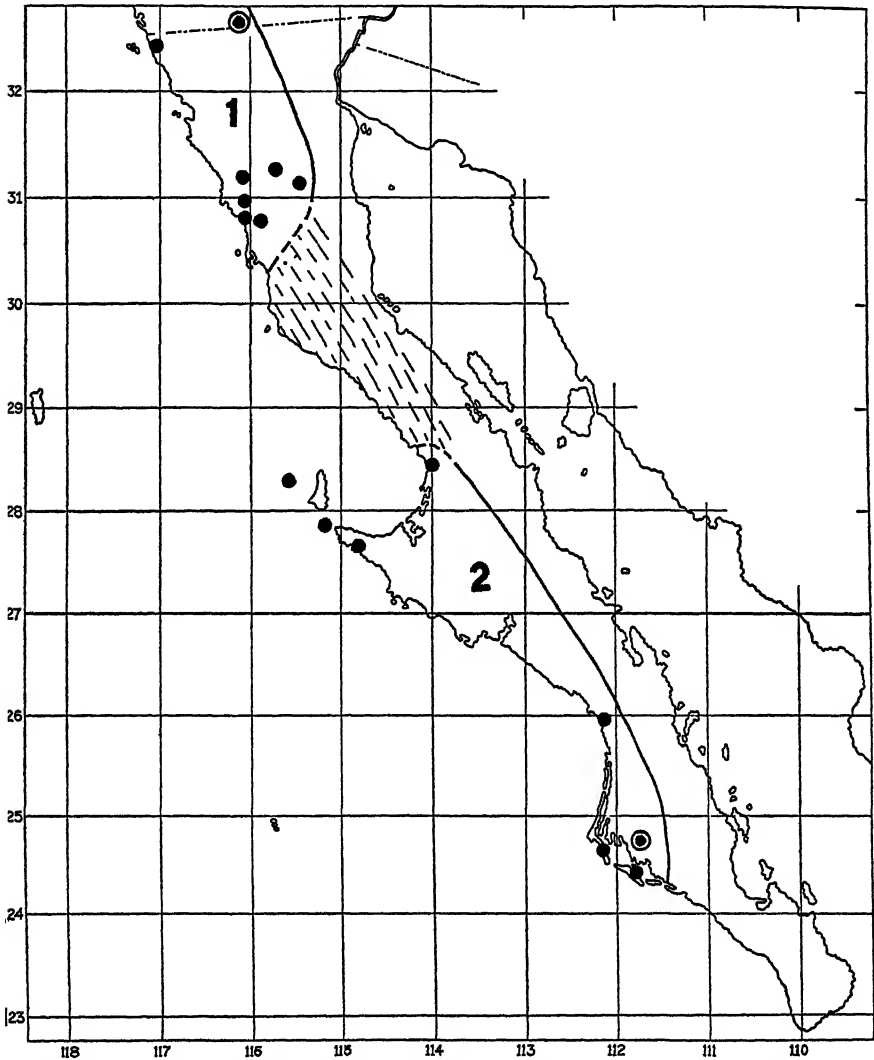
Fig. 5. Distribution of races of horned larks in Lower California: 1, *O. a. actia;* 2, *O. a. enertera.* Plain dots indicate localities from which breeding specimens have been examined; encircled dots indicate type localities. Intergradation between the two races is indicated by broken lines.

Desert. The plain is fertile and mostly covered with an abundant growth of desert vegetation. The type locality of the race is at the southern end of the plain in an open prairie about 10 miles long in an east and west direction and from 3 to 4 miles broad, with its western end near the sand dunes on the east shore of Magdalena Bay. Speaking of this type locality, Nelson (*op. cit.,* p. 72)

says: "Immediately inland from the shore of Magdalena Bay is a shallow, nearly level sink . . . which becomes flooded in times of heavy rain. It is known locally as the Llano de Yrais and is mainly free from the heavy growth of desert vegetation common to the surrounding plain, thus giving it an open, prairie like appearance."

Distribution and variation.—Although the race *enertera* has been regarded by some students as poorly differentiated, it appears to me to be rather distinct, in its combination of pale coloration and small size. The latter feature differentiates it from all neighboring races. The color is of considerably paler tone than that of *actia* in typical form, but the two races do blend together over a rather large area. In coloration, *enertera* is close to *ammophila*, but, curiously, the rather distinct race *leucansiptila* lies between the two. Here, then, we have an example of the fairly common circumstance in horned larks, namely, a greater resemblance in coloration between distant races than between immediate neighbors.

As we have observed in connection with *actia*, dark specimens of that race occur in the San Pedro Mártir region of northern Lower California. Southward from this area of heightened intensity of color there sets in a trend of progressive pallor, which finally culminates in the race *enertera*. The first indications of this trend in *actia* are seen in specimens from south and west of the San Pedro Mártir region, namely, from San Telmo, Santo Domingo, and San Ramón. Specimens from these localities are very slightly paler than birds from the San Pedro Mártir region, although still close to *actia*.

A series of twelve specimens taken January 9 and 10, 1931, at San Agustín are, as a group, pale and might equally well be called *actia* or *enertera*, for they are composed of various degrees of intermediates. Oberholser (1902:848) speaks of specimens from San Fernando, a nearby locality, as being slightly paler but "referable clearly to *actia*." Specimens present from Santa Rosalía Bay are very pale and typical of *enertera*. Hence the transition from *actia* to *enertera* occurs gradually over a long area from just south of San Ramón to the Playa María Bay region. The most characteristic example of *enertera*, then, occur from Santa Rosalía Bay south to Magdalena Bay.

Examples taken from San Benito Island, Natividad Island, and Turtle Bay are referable to *enertera*. One breeding bird from San Benito Island, though darker than the others and thus approaching *actia*, is nevertheless to be regarded as an extreme of *enertera*. Since the specimens from the three mentioned localities as well as those from Santa Rosalía Bay are so pale, the true area of intergradation with *actia* seems to be somewhat farther north than Grinnell (1928:145) has mapped it.

Because of the gradual trend of intergradation with *actia*, the winter wandering of individuals, and individual variation, series collected in winter in one locality often show several stages of intergradation. This is true of the series in the Museum of Vertebrate Zoölogy from Santo Domingo taken in December, of the San Agustín series taken in January, and, to a lesser degree, of the series in the Dickey collection from Natividad Island taken in December. As Grinnell (1928:144) points out, both *actia* and *enertera* have several times

been recorded from the same place, the probable explanation being the difficulty of naming intermediate specimens and the wandering of individuals during nonbreeding times. The specimen referred to *insularis* by Lamb (1927:70) and to *actia* by Grinnell (1928:144) is simply a stained example of *enertera*.

The bills of the males of the Llano de Yrais series seem to be uniformly more curved and actually measure longer than those of the more northern representatives; the upper mandibles taper to a sharper point and curve downward more sharply. Seven breeding males from the Santa Rosalía Bay area average 9.1 mm. in bill length from nostril; sixteen from Santa Magdalena and vicinity average 9.7 mm. If these specimens were young birds, we might assume this terminal sharpness and increased curvature to be representative of the condition before wear tended to blunt the end. The series is composed, however, of breeding birds taken in April. Bills of molting juveniles of other races fail to show any such accentuation of bill curvature or of elongation of the terminal part as we see here. This structural peculiarity is apparently indigenous to the horned larks of the Santa Magdalena region. Indeed, it differentiates this local population from all other representatives of the race that I have examined.

Extreme variation among juveniles has been encountered in this race. This scarcely can be accounted for on grounds of geographic variation alone, for the most variable juveniles, that is, those that show the greatest extremes, are all from the Santa Magdalena region. Individuals characterized by such contrasting colors as pale gray, or brown, or dusky serve to bring home with some force the danger of error in defining ranges of races on the basis of only one or two juveniles.

Otocoris alpestris adusta Dwight

Scorched Horned Lark

Otocoris alpestris adusta Dwight (1890:148), original description, part; Bendire (1895:345); Oberholser (1902:858); Swarth (1904:28); Swarth (1905:79); Ridgway (1907:325); Swarth (1914:44); Bailey (1923:32); Swarth (1929: 311); Law (1929:219); van Rossem (1931:266); van Rossem (1936b:139)

Eremophila alpestris adusta, Bangs (1930:367)

Chionophilos alpestris adustus, Hellmayr (1935:8)

Type.—Adult male, no. 223575, Mus. Comp. Zoöl. (no. 23575, William Brewster collection); Camp [Fort] Huachuca, Santa Cruz County, Arizona; February 21, 1887; collected by J. C. Cahoon.

Dwight (1890:148) described four cotypes, one of which Oberholser (1902:858) designated as the type. Bangs (1930:367) listed all four cotypes, refusing to recognized any single one as a holotype.

Diagnosis.—Characterized by a strong "scorched" brown appearance, which distinguishes this race from all others; hence darker, more brownish than *leucansiptila* and *aphrasta*; lighter brown, more tawny, and smaller than either *occidentalis* or *leucolaema*. In fresh plumage, nape and back practically concolor, averaging Snuff Brown. In worn breeding plumage the nape may be Tawny or even Onion Skin Pink; the back is commonly Pecan Brown, though often Orange Cinnamon.

Measurements (in millimeters).—Breeding males (49 specimens): wing, 101.0 (105.4–95.3); tail, 68.3 (73.2–62.3); bill from nostril, 9.2 (10.1–8.1); tarsus, 20.8 (22.0–19.5); middle toe without claw, 10.1 (11.5–8.7).

Breeding females (19 specimens): wing, 93.4 (97.6–92.0); tail, 60.2 (63.1–56.0); bill

from nostril, 8.4 (9.1–7.5); tarsus, 20.2 (20.8–18.1); middle toe without claw, 10.0 (10.8–8.7).

Distribution.—Resident in central southern Arizona from Tucson and vicinity south at least to Mexican border; western limit as now known is east base of Baboquívari Mountains; from there the breeding range extends eastward to extreme southwestern corner of New Mexico.

Specimens examined.—Material representative of this race amounts to 108 skins, of which 53 are breeding males, 20 breeding females, 27 autumn and winter males, 7 autumn and winter females, and 1 a juvenile. These skins were taken at the following localities. Those marked with an asterisk are localities from which breeding birds were taken. Unless otherwise indicated, the specimens are in the Dickey collection.

ARIZONA. Pima County: East slope Baboquívari Mts.*, 1; Altar Valley*, 1; Fort Lowell, 1; 20 mi. W Tucson*, 1 (Santa Barbara Mus.). Santa Cruz County: Patagonia*, 8; 10 mi. N Patagonia*, 8 (Univ. Arizona coll.); 5 mi. W Ruby*, 1; Arivaca*, 1; Atasco Mountains*, 10; Fort Huachuca*, 10 (Dickey coll.), 7 (Mus. Vert. Zoöl.); Huachuca*, 4 (Dickey coll.), 3 (Univ. Arizona coll.). Cochise County: 6 mi. NE Light P. O., Sulphur Springs Valley*, 1 (Law coll.); 3 mi. N Riggs Ranch, 5000 feet, Sulphur Springs Valley*, 1 (Law coll.); Pinery Canyon, Chiricahua Mts.*, 28 (Law coll.); White-tail Canyon, Chiricahua Mts.*, 1; Wilcox*, 4 (Stanford Univ. coll.); 10 to 15 mi. SE Dos Cabezos, 14 (Law coll.); 5 mi. NW Pierce*, 2 (Univ. Arizona coll.).

NEW MEXICO. Hidalgo County: Rodeo*, 1 (Law coll.).

Habitat notes.—The race *adusta* occurs in a section of Arizona and New Mexico that is part of the great Sonoran Desert. This area is one of high summer and low winter temperatures. It is characterized by widely spaced plants with considerable areas of bare ground. The characteristic vegetation shows much heterogeneity. Some of the more conspicuous types are the giant cactus, cholla, mesquite, catclaw, ocotilla, and creosote bush. Over much of the range, desert grass is absent, but in extreme southeastern Arizona there are some grassy plains where horned larks of this race are abundant.

Distribution and variation.—Representatives from the range of *adusta* present a more uniform appearance than usual in races of horned lark. Even so, there are indications of some local variation within the race. Skins showing the greatest degree of differentiation, that is, skins which are most typical of the race, come from the vicinity of Fort Huachuca, which is also the type locality. Examples from Fort Huachuca show the greatest amount of brown and appear most intensely "scorched." From this center, extending outward to the east and west, there seems to be a gradual tendency toward paleness of the dorsum, while at the same time the nape color tends to become more prominent. Probably a similar modification of characters occurs southwardly where *adusta* intergrades with *aphrasta*. The reverse trend likely occurs to the north, where *adusta* joins the much darker brown, unscorched *occidentalis*.

Four of nine breeding males from the Atasco Mountain region in Santa Cruz County, Arizona, west of the type locality are slightly paler than the others. This might be interpreted as indicating an approach to *leucansiptila*, the next race to the west, were it not for the fact that examples taken still farther west are again darker, and typical of *adusta*.

According to our present knowledge, there is a large area between the ranges of *leucansiptila* and *adusta* in which no breeding horned larks occur. According to van Rossem (1936b :124), along the United States–Mexican border west

of the Baboquívari range there is a terrain of broad, level country with grassy plains in valleys separated by stony ridges or low mountains. In all probability, horned larks do occur in such valleys. It may even be that the type of *pallida* is an intergrade between these two races in such an intermediate area. In other words, there is no known reason why breeding horned larks should not occur in the seeming gap between *adusta* and *leucansiptila*.

Concerning the region of contact between *adusta* and *occidentalis*, it is known that *adusta* ranges as far north as Tucson; a breeding specimen from twenty miles west of there resembles topotypes. The intergradation with *occidentalis* must, then, occur north of Tucson. Many fall and winter examples, collected by Swarth and now in the California Academy of Sciences collection, seem to be intermediate, in various degrees, between these two races.

Oberholser has assigned the extreme southeastern corner of Arizona to the range of *aphrasta*. He has stated (1902:862) that breeding birds from Wilcox and Fort Bowie, Arizona, show an inclination toward *leucolaema* in the pallor of the occiput and nape, but should be placed with *aphrasta*. On the basis of juveniles, he assigned, at the same time, Sulphur Spring and Willow Spring valleys to the range of *aphrasta*. Curiously, several specimens at hand taken in early March, 1919, at Wilcox are very pale, as Oberholser states his examples to be. But there is no reason to believe that these were breeding birds or that they were even on the breeding grounds of horned larks.

Presenting evidence quite to the contrary are certain breeding examples from several localities in this general area; these are typical of *adusta* in every way. In the Law collection, a series of twenty-eight skins from Pinery Canyon in the Chiricahua Mountains is completely made up of birds typical of *adusta*. Many of these were taken in early March, but some have later dates, in April and May. Also in the Law collection are two specimens from Sulphur Spring Valley taken in June and July. No. 7445, male, July 9, 1919, is from 6 miles northeast of Light Post Office. The other, no. 8214, male, June 23, 1921, is from 3 miles north of Riggs Ranch, 5000 feet. Both of these are unquestionably *adusta*. A breeding male and female from Rodeo, New Mexico, nos. 903 and 904, Law collection, April 28–29, 1913, are again typical of *adusta*, despite the fact that Bailey (1928:452) states that *aphrasta* has been taken at "Rodeo, April 1913 (Law and Brooks)," a statement which probably refers to the very specimens mentioned above.

Fraught with more significance is the fact that four breeding males from Wilcox, in the Stanford University collection, are good examples of *adusta*, differing from topotypes of that race only in their slightly paler occipital and nape regions. Thus, it seems that *adusta*, not *aphrasta*, is the breeding race of extreme southeastern Arizona and extreme southwestern New Mexico. The pale specimens from Wilcox, mentioned above, may, however, be of the race *aphrasta* and so constitute nonbreeding records for the state. In the absence of comparative material. I am not prepared to declare their identity. If *leucolaema* ranges south of that form and west to the Arizona line, it may well be that *leucolaema* and *adusta* come in contact, with consequent intergradation north and east of Wilcox.

It will have become apparent by now that the exact limits of the range of *adusta* still remain more or less obscure, as do the areas of intergradation with surrounding races. A phase about which more is known, perhaps, but about which at the same time some misunderstandings have arisen, is the relationship of this race to the faunal areas in that part of the country. Swarth (1929) apparently depended greatly on the distribution of this race as one of the determining factors in his decision as to where to draw the line between his "Western Desert Area" and his "Eastern Plains Area." At the time of his work, *adusta* was known to extend westward only as far as the Santa Rita Mountains and was thought to be characteristic only of the plains area. Accordingly, the line dividing the two areas was drawn at the Santa Rita Mountains. Swarth's Eastern Plains Area is characterized by grassy, rolling hills or gently sloping plains, whereas the Western Desert Area is characterized by an arid type of shrubbery of isolated clumps separated by bare ground. Grass is almost entirely lacking. The material in the Dickey collection proves, as van Rossem (1936b:139) has pointed out, that *adusta* occurs much farther west than Swarth thought; it extends at least as far as the east base of the Baboquívari Mountains. Hence *adusta* occurs in both of Swarth's faunal areas and so in both types of country. In all probability, however, the center of abundance of the race is in the Eastern Plains Area, a type of country which is, I would judge, better suited to its habitat requirements.

Otocoris alpestris occidentalis McCall

Montezuma Horned Lark

Otocoris? occidentalis McCall (1851:218), original description
[*Otocorys alpestris*] *arenicola* Henshaw (1884:259), part
Otocoris alpestris arenicola, Merriam (1890:94); Bendire (1895:338), part
Otocoris alpestris adusta Dwight (1890:148), part
Otocoris alpestris occidentalis, Stone (1899:21); Oberholser (1902:855); Ridgway (1907:324); Swarth (1914:44); Bailey (1928:452); Swarth (1929:312)

Type.—Juvenile, no. 14883, Acad. Nat. Sci. Phila.; Santa Fe, Santa Fe County, New Mexico; July, 1850; collected by George O. McCall.

Diagnosis.—Distinguished from *leucolaema* by darker brown coloration throughout; differs likewise from *utahensis*, totally lacking the grayish appearance of these two neighboring forms; larger than *adusta*, richer brown, and without the "scorched" appearance of that race.

Measurements (in millimeters).—Breeding males (30 specimens): wing, 104.1 (108.7–99.2); tail, 70.7 (74.3–65.6); bill from nostril, 9.1 (10.1–8.6); tarsus, 21.0 (22.5–19.2); middle toe without claw, 10.4 (11.8–9.5).

Breeding females (10 specimens): wing, 95.6 (98.5–94.3); tail, 63.3 (70.0–61.1); bill from nostril, 8.7 (9.2–8.0); tarsus, 20.6 (21.6–19.6); middle toe without claw, 9.8 (10.4–9.4).

Distribution.—Breeds in central and northern Arizona, thence east to central New Mexico, where intergradation takes place with *leucolaema* in the vicinity of Santa Fe. Some members of the race evidently winter within the breeding range, but there is said also to be a partial southward migration to central western Texas, northern Chihuahua, and Sonora.

Specimens examined.—Skins examined referable to this race total 196. Of these, 47 are breeding males, 23 breeding females, 83 autumn and winter males, 32 autumn and winter females, and 11 juveniles. The following localities are represented. Unless otherwise indi-

cated, specimens are in the Randolph Jenks collection. Localities marked with an asterisk are represented by examples taken during the breeding season.

NEW MEXICO. Santa Fe County: 1 mi. S Santa Fe*, 6 (Mus. Vert. Zoöl). Bernalillo County: Albuquerque*, 6 (U. S. Nat. Mus.). Grant County: 3 mi. N Gila*, 2. Catron County: 5 mi. NE Glenwood*, 4.
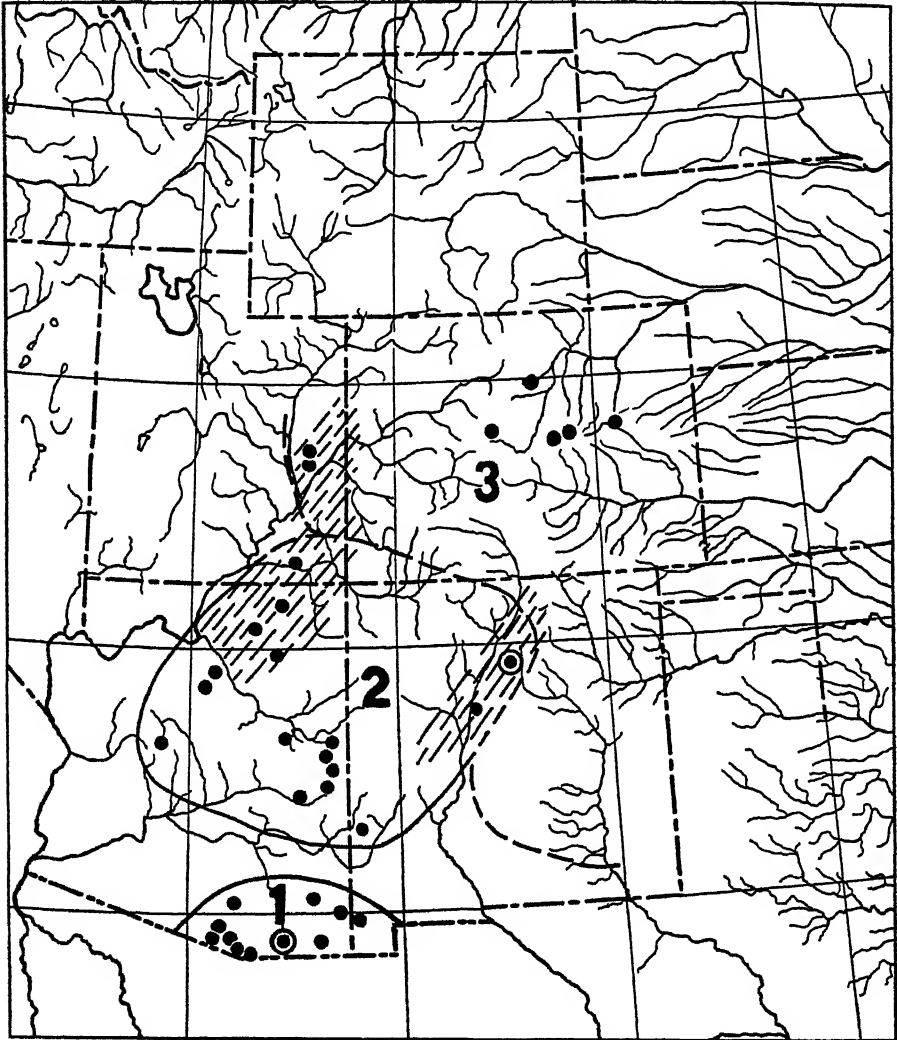
Fig. 6. Breeding ranges of certain races of horned larks in the southwestern United States: 1, *O. a. adusta;* 2, *O. a. occidentalis;* 3, *O. a. leucolaema* (part). Plain dots indicate localities from which breeding specimens have been examined; encircled dots represent type localities. Areas of intergradation as evidenced by material examined are indicated by broken lines. Intergradation between *adusta* and *occidentalis* probably occurs, although no breeding specimens were at hand from the intermediate area.

ARIZONA. Navajo County: Kayenta*, 2 (Mus. Northern Ariz.) ; Tonaleo*, 1 (Mus. Northern Ariz.) ; 8 to 16 mi. SE Polacca, 5800 ft.*, 3 (Mus. Vert. Zoöl.) ; 5 to 15 mi. SE Holbrook, 5250 ft., 7; 9 mi. N Snowflake*, 12. Coconino County: Cameron Bridge road, 28 mi. NNE Flagstaff, 1 (Mus. Vert. Zoöl.) ; Merriam's Crater, San Francisco Mts., 1 (Mus. Northern

Ariz.); Black Hawk Valley, San Francisco Mts., 6 (Mus. Northern Ariz.); Long Lake, Anderson Mesa, San Francisco Mts., 1 (Mus. Northern Ariz.); Canyon Padre, San Francisco Mts., 1 (Mus. Northern Ariz.); Babbitt's Tank, 30 mi. E Flagstaff, San Francisco Mts.*, 2 (Mus. Northern Ariz.). Yavapai County: Lonesome Valley, near Prescott*, 27 (Univ. Ariz.). Apache County: Vicinity of Springerville*, 3 (Univ. Ariz.), 20 (Jenks coll.); 13 mi. S Springerville, 9000 ft., 2; 1 mi. W Eager, 6900 ft., 2; Voigt Ranch, 6 mi. SSE Greer*, 1 (Mus. Vert. Zoöl.), 16 (Jenks coll.); Big Lake, White Mts., 20 mi. S Springerville*, 4 (Mus. Vert. Zoöl.); Crescent Lake, 9000 ft., White Mts., 21 mi. S Springerville, 8; Summit Baldy Peak, 12,500 ft., White Mts., 1; Basin Lake, 9000 ft., White Mts., 7; Black River, 9000 ft., E base Baldy Peak, White Mts., 2; 3½ mi. E Phelps Ranger Station, 7 mi. E Baldy Peak, 9000 ft., White Mts.*, 6; 1 to 3 mi. NE Baldy Peak, White Mts.*, 3. Gila County: 2 to 8 mi. SW White River, 21; 1 mi. N San Carlos, 4; 8 mi. S San Carlos, 9.

Distribution and variation.—The most typical examples of *occidentalis* are from the White Mountains region of central eastern Arizona. Examples taken during the breeding season from various localities in this area are extremely brown over the entire back and nape regions. In this characteristic they are noticeably distinct from *leucolaema*. Specimens in fresh fall plumage from this same area are characterized by a deep rufescent shade, which is particularly noticeable in the nape region. The autumn examples, however, show less pronounced differences from *leucolaema* than do breeding birds. Thus we have an exception to the rule that the racial differences in horned larks are most apparent in fresh fall plumage.

Oberholser stated that birds from Fort Verde, Arizona, were the most representative of the race. A series of specimens in fresh fall plumage from the nearby Prescott region are less differentiated from *leucolaema* than are the White Mountains examples. Oberholser also referred examples from the San Francisco Mountains to *occidentalis*. One or two breeding birds from there and some early fall molting examples that I have examined are again not as clearly differentiated from *leucolaema* as are those from the White Mountains. Although the San Francisco Mountains examples are perhaps closest to *occidentalis,* they differ but little from Colorado examples of *leucolaema* in comparable stages of plumage. They look to be in a transitional stage toward the latter race. This blending between *occidentalis* and *leucolaema* seemingly occurs in central northern Arizona and in the Painted Desert region of the northeastern part of the state. Breeding specimens from Polacco, Navajo County, and Tonaleo, Coconino County, Arizona, are also more or less intermediate between the two races. Furthermore, these examples and others show similarities to birds from southeastern Utah, previously discussed, which show an approach to *occidentalis*. Incidentally, the migrant examples from northern Arizona, reported by Hargrave (1936:121) as *lamprochroma,* prove to be the same as birds from this southeastern section of Utah. They are not at all like examples of *lamprochroma* from Nevada or Oregon.

Breeding birds from the Springerville region, Apache County, Arizona, show local differences in possessing a slightly more pallid dorsum and a decidedly pinkish nape. In these variations they show an approach to *leucolaema,* but this appearance is difficult to reconcile with the distribution of the two races. The Springerville examples were taken in April at 6900 feet, and the

locality is but a short distance from Greer and other White Mountains locali-
ties where typical *occidentalis* has been taken. Furthermore, other fairly typi-
cal examples of *occidentalis* have been collected from localities all around
Springerville. Breeding examples from three miles north of Gila, Grant
County, five miles northeast of Glenwood, Catron County, and from Albuquer-
que, Bernalillo County, are certainly referable to *occidentalis*.

In eastern New Mexico, *occidentalis* again blends with *leucolaema*, produc-
ing intergrades similar in appearance to specimens from northeastern Ari-
zona and southeastern Utah. Topotypical specimens from Santa Fe, New
Mexico, are among these intergrades.

SUMMARY OF GEOGRAPHIC VARIATION

From the accounts of the various subspecies here presented, it is apparent that
the different races are far from being the precise units that our nomenclatural
system would indicate. Furthermore, it is evident that different degrees of
differentiation are represented in the several races studied. Only one race,
arcticola, is sufficiently differentiated to show no intergradation or overlap
in characters with any other race. Of the subspecies that do show intergrada-
tion, there are two general types. Some, like *rubea* and *adusta,* are well marked
with distinctive characters, and intergradation with adjacent forms is more
or less abrupt. Then there are weakly developed races like *ammophila,* which
show a maximum amount of intergradation with all neighboring races. Be-
sides these named races there are many less strongly differentiated local popu-
lations within the range of almost any of the subspecies. We have, then, in
Otocoris alpestris, a widespread, highly variable species, constituting a Ras-
senkreis. The distinctive populations are connected for the most part by in-
termediate populations, and between the centers of differentiation blending
occurs, except where effective barriers are present to prevent intergradation.

The distinction between the locally varying populations and the various
stages of differentiation represented by the geographic races of horned larks
seems to be one mainly of degree of differentiation and geographic extent of
the variation. Just as the species is made up of many subspecies, so are the
subspecies composed of a mosaic of locally varying populations. No sharp
distinction between species, subspecies, and locally varying groups is pos-
sible, and we seem to have a sequence of steps leading to the formation of the
full species. That is to say, the local variations seem to be on the way to becom-
ing subspecies; the subspecies seem to be incipient species. I have gained the
impression from my studies that the Rassenkreis *O. alpestris* is at a relatively
young stage in the speciation process.

Perhaps the most significant aspect of the geographic variation of the horned
larks is the frequency and extent of intergradation connecting the variable
units making up the species. Another important feature seems to be the differ-
ences in types of intergradation involved. A blending type of intergradation
is the commonest. This manifests itself frequently in long geographic trends
in the several characters of the birds and almost invariably occurs where the
physiography is essentially uniform and where there is an absence of mechan-

ical barriers. This is illustrated in the Great Valley of California, where, from north to south, a gradual transition occurs from *rubea* through part of *actia* to *ammophila*. In Lower California, *actia* gradually blends to the south into *enertera*. In the northwestern part of the Great Basin and in the Columbia River section, *merrilli* and *lamprochroma* seem to blend over a wide area; in the central part, *lamprochroma* and *utahensis* show a wide belt of intergradation. Similar intergradation again occurs between *utahensis* and *leucansiptila*, and between *lamprochroma* and *ammophila*.

This blending type of intergradation may conceivably have developed through gradual interbreeding of racial stocks; but to me the alternative idea of intermediate geographic differentiation is the more plausible, considering the many groups of local differentiates that seem to have developed in response to peculiar local conditions.

If the blending type of intergradation has been brought about by intermediate geographic differentiation, then a distinction must be made between that and the type of intergradation produced by different populations coming together and interbreeding. This latter process probably accounts for certain occurrences of increased variability where the peripheries of the ranges of two or more races come together. We have a suggestive example that probably comes under this category in Lassen County, California, where either *lamprochroma* and *sierrae*, or *merrilli* and *sierrae*, or possibly all three, come together. Possibly a similar case occurs in the Columbia River Gap through the Cascades, between *merrilli* and *strigata*. The marginal intergrading individuals may show a blending of their characters, or there may be segregation of characters, depending probably on the method of inheritance.

In addition to intergradation of the blending type, with modifications as noted, we find intergradation as a result of individual variants or morphological intermediates. These, as a result of their different degrees of variation, cause an overlap in the distinguishing characters of races. This seems to happen whether the races are immediate geographical neighbors or are far separated geographically. Intergradation of this type is especially common between weakly differentiated races. Thus we find intergradation by way of individual variation common in the adjacent races *merrilli* and *lamprochroma* as well as between closely related races that are distantly separated, such as *strigata* and *insularis*, and *sierrae* and *strigata*.

It would seem that intergradation in the races of horned larks is influenced by several things. On the one hand, we have internal factors in the organism. One of these is the inherent genetic variability of each race, resulting in individual variation which may or may not produce intergradation between races. The degree of differentiation of a population or race is a factor here, too, for there is less overlap between strongly differentiated races. As illustrative of the importance of the genetic nature of the racial characters, there are the races *sierrae* and *strigata*. On the basis of the material at hand, the character of yellow on the underparts, which is common to these two races, seems to show alternative inheritance, without any blending.

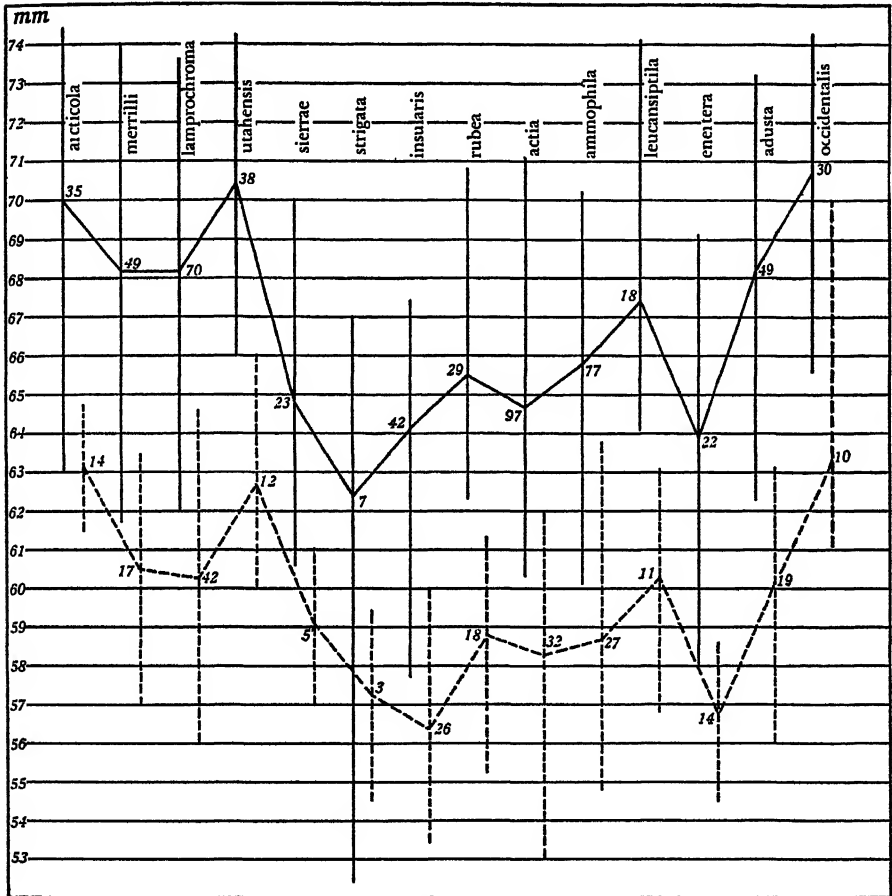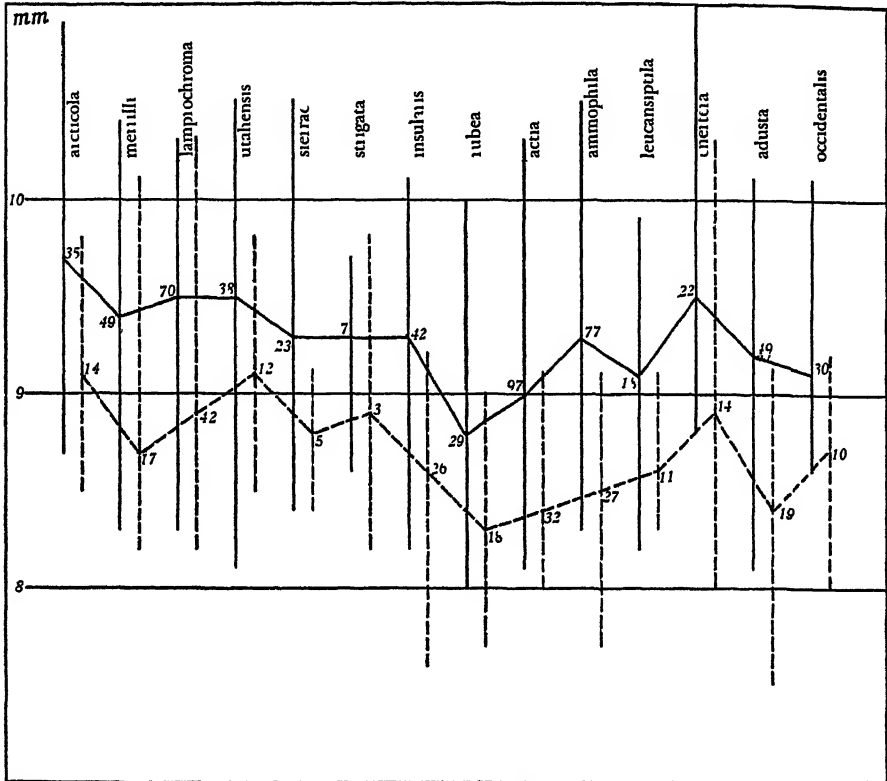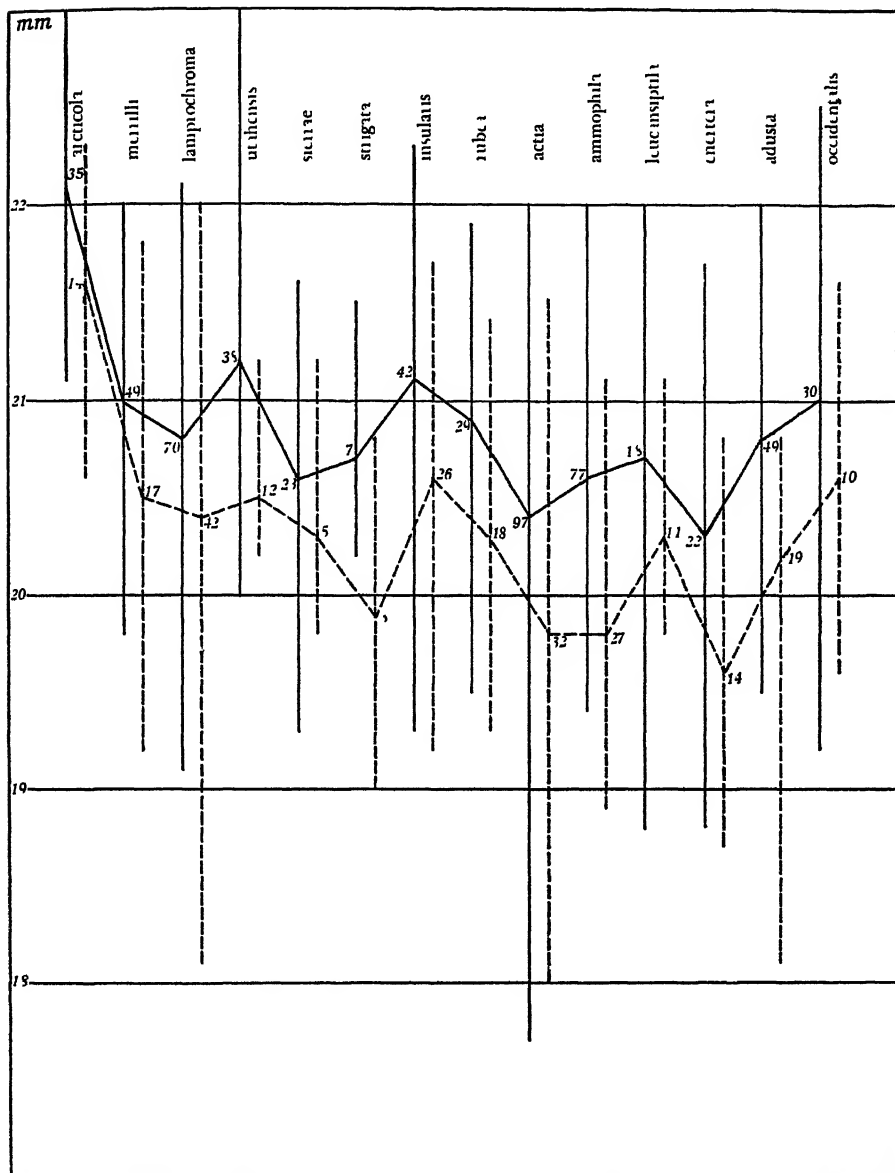On the other hand, the role of the environment is an important considera-
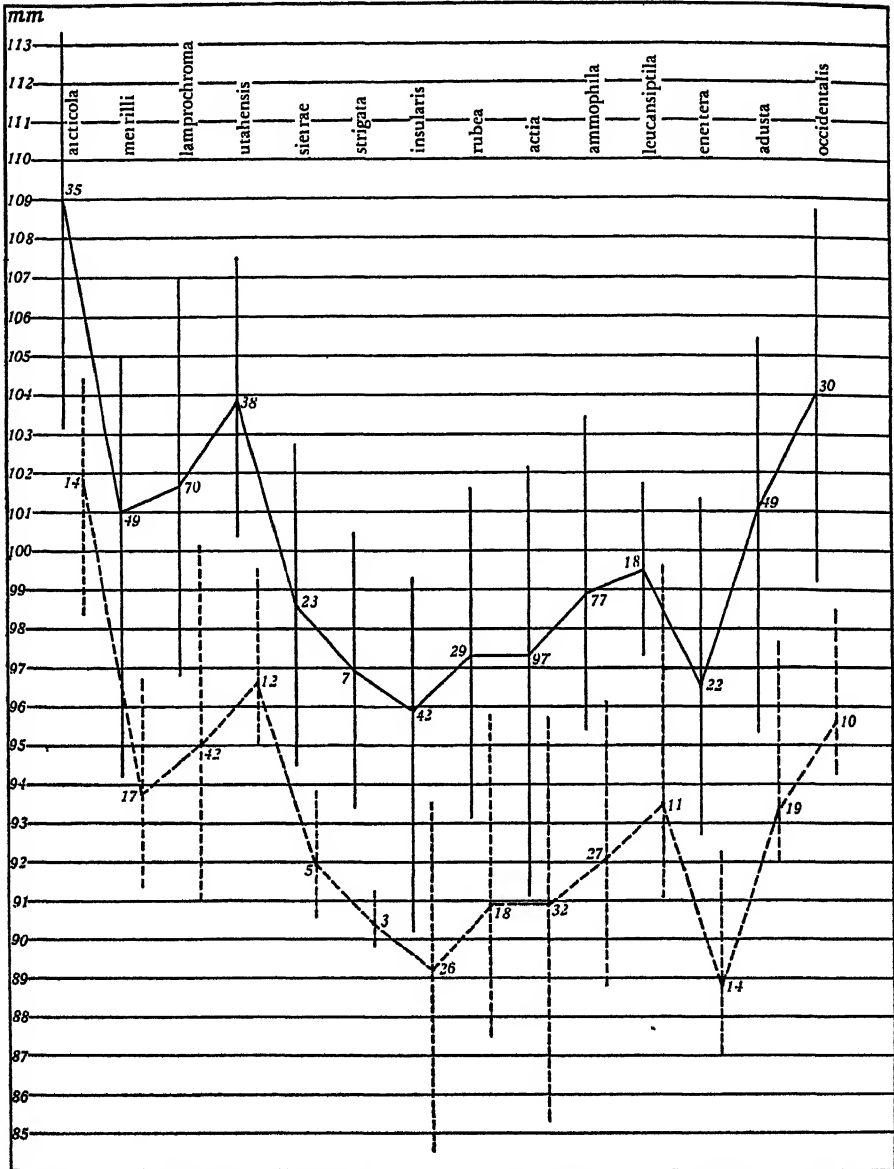
Fig. 7. Diagram showing individual, sexual, and geographic variation in length of wing of adults of fourteen races of horned larks. Solid lines, males; broken lines, females; figures at right or left of these lines indicate numbers of individuals measured; length of lines shows range of individual variation; points connected by solid and broken lines mark positions of averages.

tion, as shown by the fact that mechanical barriers tend to prevent intergradation of the blending type. Associational barriers also prevent contact of races. Continuous open country is often conducive to blending intergradation; broken country, forest, and grassland, a hindrance. Environmental differences, furthermore, either directly or indirectly, are factors making for intergradation in that they participate in the production of intermediate

differentiation in areas which are geographically intermediate between main centers of differentiation.

Even though the geographic races here recognized by name are characterized by certain combinations of characters, we must appreciate their widely intergrading tendencies. What, then, of the trends of variation in characters over geographic areas greater in scope than the range of any one or two geo-
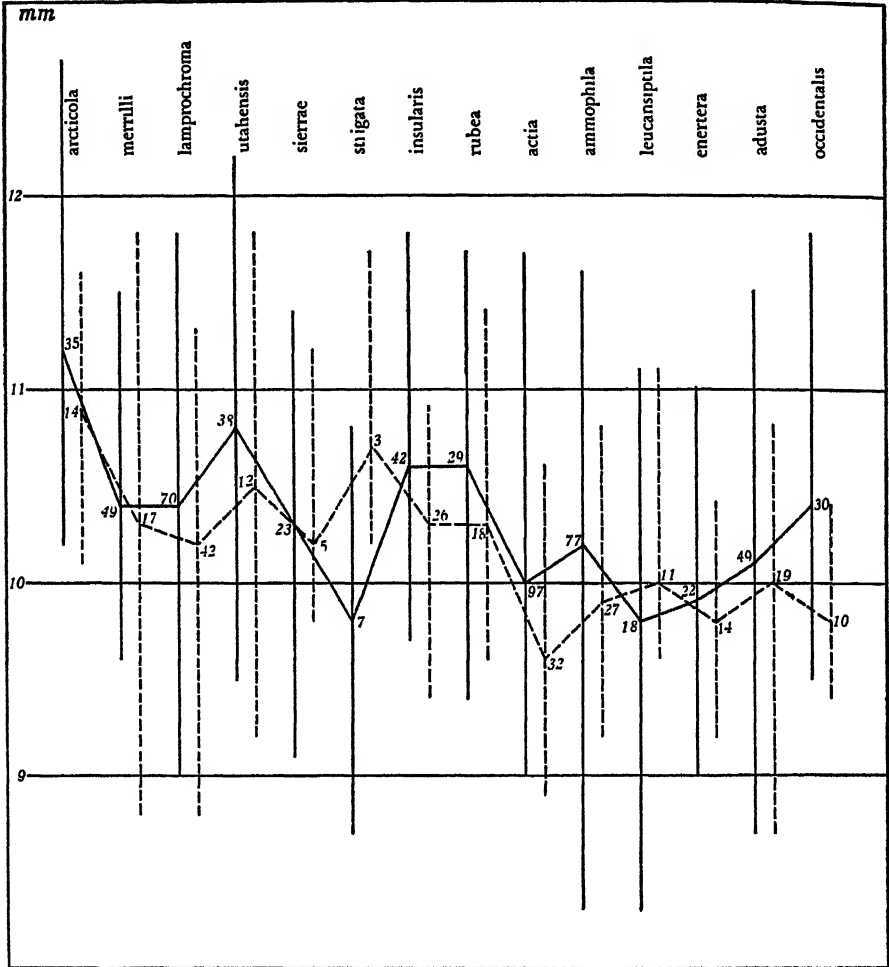

Fig. 8. Diagram showing individual, sexual, and geographic variation in length of tail of adults of fourteen races of horned larks. Solid lines, males; broken lines, females; figures at right or left of these lines indicate numbers of individuals measured; length of lines shows range of individual variation; points connected by solid and broken lines mark positions of averages.

graphic races? Of the measurable characters in horned larks, the one which shows the greatest range of variability and the most significant differences between races is wing length. The northern race *arcticola* is distinctive in having the longest wing. More noteworthy is the fact that *arcticola* and the neighboring race *merrilli* show little if any overlap in this character, the difference in average wing length being about eight millimeters. The race *utahensis* measures larger than *merrilli* and, even though separated geographically

from *arcticola,* shows a slight overlap with *arcticola* in this character. *Merrilli* and *lamprochroma* have about the same average length of wing. *Sierrae* is slightly smaller than *merrilli.* The races *actia* and *ammophila* are next in order of diminishing size and present a situation similar to that between *merrilli* and *lamprochroma,* since they average about the same. The small size of *strigata* is outstanding, while the race with the smallest wing length of all

Fig. 9. Diagram showing individual, sexual, and geographic variation in length of bill from nostril of adults of fourteen races of horned larks. Solid lines, males; broken lines, females; figures at right or left of these lines indicate numbers of individuals measured; length of lines shows range of individual variation; points connected by solid and broken lines mark positions of averages.

is *insularis.* The island form averages even smaller in wing length than does *enertera* from Lower California.

The geographic variation in tail length follows, in general, the same trends as it does in wing length. One or two departures stand out, however. There is less difference between the average tail lengths of *arcticola* and *merrilli* than there is between their wing lengths. The small sample of *utahensis* shows a slightly longer tail than does *arcticola.* The overlap, caused by individual variation, between *arcticola, merrilli, lamprochroma,* and *utahensis* is considerable. *Strigata* has a slightly shorter tail than has *insularis.*

In length of bill, *arcticola* again averages the longest, though very little

Fig. 10. Diagram showing individual, sexual, and geographic variation in length of tarsus of adults of fourteen races of horned larks. Solid lines, males; broken lines, females; figures at right or left of these lines indicate numbers of individuals measured; length of lines shows range of individual variation; points connected by solid and broken lines mark positions of averages.

more than *merrilli, lamprochroma,* and *utahensis* which are essentially the same. *Sierrae, strigata,* and *insularis* all have about the same averages. We find *rubea* has a somewhat shorter bill, but *enertera* has a bill length equal to that of *utahensis.* This last fact is surprising in view of the smallness of *enertera* in other dimensions. In this character we have an exception to the general trend of decrease in size southward.

The three largest averages for tarsal length are, in order, *arcticola, utah-ensis,* and *insularis.* The relatively great difference between *arcticola* and *merrilli* again shows up. *Lamprochroma* is slightly smaller than *merrilli,* and *sierrae* smaller than *lamprochroma.* The average tarsal length of *strigata*

Fig. 11. Diagram showing individual, sexual, and geographic variation in length of middle toe without claw of adults of fourteen geographic races of horned larks. Solid lines, males; broken lines, females; figures at right or left of these lines indicate numbers of individuals measured; length of lines shows range of individual variation; points connected by solid and broken lines mark positions of averages.

lies between those of *merrilli* and *sierrae.* An interesting fact is the greater length of tarsus found in *insularis* when compared with neighboring main-land forms. This is associated with smaller wing length, which by inference indicates increase in use of the foot on the islands and less emphasis on flight. The smallest average length of tarsus, in *enertera,* is in keeping with decrease in size of wing and tail. In most of its characters, *ammophila* aver-ages slightly larger than *actia,* this being true also for tarsal length.

Size of middle toe varies in much the same way as does tarsal length. *Arcticola* has the longest average measurement for this character; *merrilli* and *lamprochroma* average about the same, whereas *utahensis* is slightly larger, being intermediate between *merrilli* and *arcticola*. *Strigata* proves to be small, as usual, whereas *insularis* is longer in this respect than *strigata* or *actia*. Insular conditions, again, seem to be conducive to longer toes as well as longer tarsus and shorter wing. *Leucansiptila*, for once, averages smaller in length of middle toe than does *enertera*, while both average smaller than does either *actia* or *ammophila*.

Thus, to summarize, *arcticola* is the largest race of the group. Next in order of decreasing size is *utahensis*, which is intermediate between *arcticola* and *merrilli*. *Lamprochroma*, we have seen, differs very little from *merrilli*. *Sierrae*, on the other hand, is smaller than *merrilli* but larger than *strigata*. *Strigata* is small, but *insularis* is even smaller. *Rubea* and *actia* have about the same average measurements, but *ammophila* is slightly larger, as is *leucansiptila*. *Adusta* is large, slightly larger than *leucansiptila*. *Enertera* is the smallest mainland representative of the species studied.

It appears that there is a general correlation between all the characters measured. *Arcticola*, for instance, not only has the largest wing, but also the longest tail, bill, tarsus, and middle toe. *Lamprochroma* and *merrilli* not only agree in having the same wing length, but all their other measurable characters are about the same. The same correlation holds true for other races with but a few exceptions. The greatest difference between any two neighboring races is to be seen when *arcticola* and *merrilli* are compared. This shows up best in average wing length, but differences in nearly all the other characters are proportionately as great.

The races show a pronounced trend of decreasing size from north to south, with maximum size in *arcticola*, minimum in *enertera* and *insularis*. The transition from *arcticola* to *merrilli* is rather abrupt in the Cascade mountain range. South through the Great Basin the trend is more gradual. From *arcticola* through *utahensis*, *occidentalis*, and *adusta*, on into Mexico, and even as far as Bogotá, Colombia, in South America, there is a steady decrease in size. South from *utahensis* through *leucansiptila* to *enertera* a similar trend is encountered. From *merrilli* through *actia* down to *enertera* the tendency again is toward decrease in size. Thus, with one exception, we find seeming conformance to Bergmann's Law, that the larger-sized individuals and races occur in the north, that is, where the temperature of the breeding season is low, whereas the smaller races occur in the warm southern regions. The one exception is the race *strigata*, which decreases in size northward along the coast from *actia*. Even within *strigata* itself this tendency is manifest.

The ratios of tail length to wing length in the different geographic groups indicate that there is no generalized correlation with migration. It is true that the migratory races have in general longer wings and tail than have the resident races, but this seems merely to be a conformance to Bergmann's Law. The relative wing length is, with two exceptions, no greater in the migratory races than in resident races. This suggests that the migrational activity

may not be any more intensive than is the everyday activity; thus the longer wing and tail might not have arisen on a selective basis in connection with migration. In the two exceptions, *arcticola* and *strigata,* there may be some environmental factor other than migration that would account for the relatively longer wing. We have noted that *arcticola* is probably subjected to a greater amount of wind than are other races. This possibly affords an explanation for its longer wing, but I know of no environmental factor with which the relatively longer wing in *strigata* could be correlated.

Since the longer-winged races occur in the more northern regions and since these races also have the longest average measurements for other appendages, horned larks, with one exception, do not show conformance to the conditions of Allen's Law, namely, that in colder climates, the extremities tend to be shorter than in closely related forms of warmer climates.

Summarizing the geographic variation of insular populations, we find that in *insularis* the bill is wider at the base, the wing length and tail length each reach a minimum, and at the same time a tendency toward increased tarsal and middle-toe length appears. Thus, it may be inferred that the insular influences are toward lessened powers of flight and increased running ability. Also, there is a manifestation of darker coloration and heavier streaking in the island form. To what extent these tendencies have been produced by present insular conditions is problematical. The close similarity of the island race to *strigata* of the humid coast belt of the Pacific Northwest in matters of darker coloration, heavy streaking on the breast, and short wing and tail length suggest that the present insular conditions may not necessarily have been instrumental in the development of the characteristics mentioned.

The most pronounced trends in color characters are seen in the color tone of the dorsum. In a very general way, there is correlation between humidity and plumage color, for the palest, most bleached appearing races occur in the arid desert areas, whereas the darkest races are found in areas of greatest atmospheric humidity or rainfall. Certain exceptions to this correlation will be noted later. The trend toward pale coloration in arid areas is best seen in southern California and Lower California. Eastward from the Santa Barbara Islands to the Colorado Desert there is a transition from a highly colored race to a lighter, more brownish race along the coast and in the mountains not far back from the coast. Finally we have the extremely pale desert races. The transition southward from *actia* to *enertera* follows a similar trend from dark to light coloration in conformance with decreasing humidity. In these respects, horned larks are no different from other vertebrates, a circumstance which suggests a common set of climatic or faunal influences working in a similar manner on many vertebrate forms.

One other feature of geographic trends in color characters is worthy of attention, though it occurs outside the area studied. This is the increase in brightness of coloration in the races of Mexico and Central America. Examples at hand of the Mexican race *chrysolaema* are much like *actia* but are more richly pigmented and brighter. In this respect, horned larks share a feature with many diverse types of birds. They show conformance with Gloger's Law,

that southern races tend to favor the black, brown, and especially rust-red colors, whereas northern forms are paler and grayer.

There are no trends, strictly speaking, within the species in the coloration of the underparts, which are white in all but two races. The exceptions are *strigata* and *sierrae,* which are more or less yellow beneath. In the former, the more southern representatives seem to lack the yellow, thus showing differentiation within the race with respect to this character. In *sierrae* the character is fairly constant throughout the range of the race, although yellow is not present in all individuals.

A noticeable trend in the color of the throat also occurs in a north-south direction. The yellow is almost entirely lacking in the extreme northern races and becomes more pronounced southward. Thus, we find members of *arcticola* with pure white throats. The race *enthymia,* although outside our geographic field, is worthy of mention in that it, too, practically lacks the yellow; in some examples, however, there is a slight wash of it. *Leucolaema* has a little more yellow in the throat region but not as much as have *utahensis, occidentalis,* and *adusta.* Both *strigata* and *merrilli* possess yellow on the throat. Of the California races, *rubea* has the yellowest throat. Again, the yellow on the throat is very pronounced in the Mexican races. Paralleling the trend in throat color is that of the stripe over the eye, particularly in males.

One fact of geographic variation is worthy of emphasis: juveniles, as well as adults, exhibit geographic variation. Variation in adult females is less conspicuous in some respects than in adult males; the females lack certain highly variable characters that are present in the males, namely, the bright color on the nape and on the bend of the wing.

In one race there seems to be an indication of geographic variation in the degree of dimorphism between the two sexes in their secondary sexual characters. This is in the race *strigata.* The few females available from the Puget Sound region are characterized by increased pigmentation on the bend of the wing, resulting in bright coloration such as is usually found in males of all races; there is also a suggestion of heightened color on the nape. Elsewhere within the range of the race the two sexes differ to the extent that is usual in other races.

One of the peculiarities of horned larks is the tendency for geographically distant races to resemble one another. Usually one or more well-marked races are interposed between the two showing the resemblance. As illustrating this I may cite several examples. *Strigata* most closely resembles *sierrae* and *insularis,* but is separated from *sierrae* by *merrilli* and from *insularis* by *actia.* *Rubea* shows, according to Oberholser (1902), a close resemblance to the race *oaxacae* of Oaxaca, Mexico, but several races are situated in the intervening territory, namely, *actia, ammophila, leucansiptila, adusta, aphrasta,* and *chrysolaema.* Not quite as widely separated are *actia* and *chrysolaema,* which also show a rather close resemblance; but even so, *leucansiptila* and *aphrasta* intervene. *Lamprochroma* and *giraudi* resemble each other more closely than each does its nearest neighbor.

In this study of the western races of horned larks certain correlations be-

tween geographical variation and altitude have been established. It has been found that variation is associated with ecologic niches which in turn are associated with different altitudinal positions. At least three instances have been noted, most conspicuous of which is that of the race *arcticola* and its range in a boreal habitat. At the southern part of its range, *arcticola* occurs only at high altitudes, whereas at lower altitudes in the same latitude another distinct race, *merrilli,* breeds. This is so in the northern Cascade Mountains. It is possible that a comparable correlation exists in the northern part of the Rocky Mountains. In the northern Sierra Nevada we find the race *sierrae* breeding at high altitudes. On the east side, in the lowlands, is *lamprochroma;* on the west side, *rubea.* A third example, although not so clear-cut, is encountered in the White Mountains region, Inyo County, California. The breeding birds in the meadows at 10,000 feet or higher seem fairly well to represent the race *lamprochroma.* Examples from the base of the mountains on either side are definitely intermediate between *lamprochroma* and *ammophila.*

Considerable geographic variation in migratory tendencies is manifest. In general, the more northern forms and the high-mountain races are migratory; the more southern ones and those at lower altitudes are permanently resident. Between the extremes we encounter races that are partially migratory. Of these, the representatives in the southern part of the range may be resident whereas those of the northern section may move down to the southern part of the range or even beyond. The races *merrilli, utahensis,* and *lamprochroma* show, in general, this type of winter movement. The races *arcticola* and *sierrae* display an altitudinal migration, moving out of their montane summer homes and frequenting the lower altitudes during the winter. The most completely migratory race is *arcticola.* Peculiar among the migratory forms is the race *strigata.* Although there is some doubt concerning the winter records for the Sacramento Valley, California, it is reported that members of the race have a definite time of departure in the fall and a definite time of arrival in the spring. There are some indications that an annual mainland-shoreward migration occurs in the race *insularis.* Individuals of this race are commonly present along the mainland coast each winter. Strictly resident races seem to be *rubea, actia, ammophila, enertera, leucansiptila,* and *adusta.*

The migratory behavior of *arcticola* and *sierrae* is undoubtedly correlated with heavy snows and lack of winter food supply. The partially migratory races may react differently each winter according to varying climatic conditions. The behavior of *strigata* and *insularis* suggests some migratory instinct carried over from the past.

Certain races, we have said, are more strongly differentiated than others. The statement has also been made that some are more uniform in their characters than are others. As a rule, those races that are most restricted in geographic range are the most distinct and show the least variation. Examples of the well-marked, uniform, and relatively restricted races are *arcticola, strigata, insularis, sierrae, rubea, enertera, leucansiptila,* and *adusta.* Highly variable and more wide-ranging are *actia, ammophila, utahensis, lamprochroma,* and *merrilli.*

We might expect the strictly resident races to be more strongly marked than the partially migratory ones, since the former are subject to the same environmental influences the year round whereas the migratory races encounter change. But this is not so; for the race which shows the best-developed migratory instinct, namely *arcticola*, is one of the best examples of a race with constant characteristics. In contrast with this, we have the strictly resident race *actia*, which is the best example of a variable race. In comparing *insularis* and *strigata* with *actia* and *ammophila*, we find the first two more strongly differentiated and more uniform. Furthermore, although closely related, each is separated from the other. This suggests the influence of the factors of age and isolation. We find that *rubea* is more strongly marked than *actia*. It has a more uniform environment than that of *actia*, at least in color of substrate, and this uniformity is probably conducive to a greater rate of selection. Thus, we see that different factors seem to have been operative in different areas and at different times. The role of some of these factors in the subspeciation of the western races is discussed in a following section.

RELATIONSHIPS OF THE RACES

With respect to phylogeny, the question arises which races are primitive and which are but lately derived. I do not think we can form any conclusions for horned larks in this respect, for there is no reason to believe that the characteristics of any one of the races are any more primitive or any more specialized than those of another. It seems to me that most of the races are products of their present environments and that they have been molded *in situ*. This seems clearly to be true of *rubea, actia, ammophila, leucansiptila, enertera, merrilli, lamprochroma, utahensis, insularis,* and doubtless of the others. No one of these races can be said to have given rise to any other race, although certain of them may have been derived from the same rather recent stock.

It may be possible to arrive at some quasi conclusions concerning the age of certain races or groups of races, but it does not necessarily follow that the older ones are ancestral or any more primitive than those of more recent origin. The races *arcticola, strigata,* and *insularis* may be older in point of time than *actia,* or *rubea,* or *lamprochroma,* but there is no reason to believe they represent the basal stock that gave rise to any one or more of the others. In other words, I do not think it possible to construct a phylogenetic tree for horned larks. At the same time, though, I do believe it possible to judge something of the relationships of some of the races; but even here there are pitfalls.

Conclusions with respect to relationships are difficult to form because it is not often known which characters are indicative of closest relationship. Similarity in general appearance is often interpreted as evidence of immediate relationship. Yet one must be mindful of the ever-present possibility that likenesses may have come about through convergent or parallel evolution in response to similar environmental conditions. Then, too, it must be remembered that closely related races may have come to be very different through the rapid accumulation of even slight mutative genetic change.

Conclusions may be drawn on the basis of the resemblance of a few char-

acters, if those characters are known to be conservative and subject to little change, but, again, detection of conservatism is not always possible. Similarity in many characters affords better evidence of relationship between races than does resemblance in few characters. Inferences as to the method of origin of races often afford supporting evidence of relationship whether or not the majority of characters are clearly indicative of relationship.
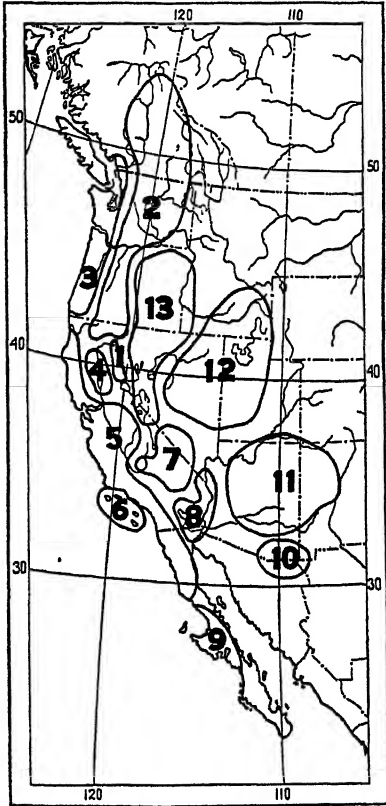
Fig. 12. Breeding ranges of thirteen of the fourteen races of horned larks studied: 1, *O. a. sierrae;* 2, *O. a. merrilli;* 3, *O. a. strigata;* 4, *O. a. rubea;* 5, *O. a. actia;* 6, *O. a. insularis;* 7, *O. a. ammophila;* 8, *O. a. leucansiptila;* 9, *O. a. enertera;* 10, *O. a. adusta;* 11, *O. a. occidentalis;* 12, *O. a. utahensis;* 13, *O. a. lamprochroma.*

Despite the many difficulties enumerated, it seems possible to find evidence of close affinity in certain of the races that we have dealt with in this study. One race seems to stand apart by itself; others appear to bear resemblance to one another, not because of any close relationship but because of convergent evolution. Mention is made in this section of one of the possible groupings of the races. Supporting data, dealing with the method of origin of certain of the races, are given in the following section.

The northern race *arcticola* seems to be removed from all others. Features of this race previously noted seem indicative of a long-standing and deep-seated endemism in a boreal habitat. They serve to mark the race as unique.

That the races *strigata* and *insularis* are closely related is suggested by their general appearance and probable origin. Although *sierrae* does not show so close a likeness to *insularis,* it has features in common with *strigata,* such as general similarity in coloration and yellow on all the underparts. This latter character has considerable significance, since it appears only in these two races. Taking into account the close resemblance of *strigata* to *insularis* and *sierrae,* we have a group of three races that presumably constitutes one late descent line; that is, they probably represent a different ancestral stock than that of any of the other races or groups of races of horned larks.

My studies on the races *actia, rubea, ammophila, leucansiptila,* and *enertera* leave me with the impression that they constitute another recent descent line, one which is quite different from that previously mentioned. These races are all similar in tones of brown and in measurements, and furthermore they grade completely into one another. The races *adusta, occidentalis,* and *leu-*

colaema probably fall together with certain eastern races to comprise another distinct stock. *Utahensis, lamprochroma,* and *merrilli* bear mutual resemblance and have contiguous ranges, and they might be considered as having been formed along still another route of descent. Thus, with reference to the area studied, the horned larks seem to have arisen from, or to comprise remnants of, several earlier stocks. With this picture in mind, let us consider some of the probable factors in the differentiation of these groups and their component subspecies.

SUBSPECIATION IN THE WESTERN RACES OF HORNED LARKS

One of the basic factors apparently responsible for evolution in horned larks is environmental change. This seems to have been responsible for a continual process of adjustment and adaptation in the organism, which has resulted in continued harmony, or approach to harmony, between the organism and its environment. Organic change seems to have been the sequel to environmental change, though the mechanism of this change may be open to much argument. A consideration of certain climatic and environmental changes apparently affecting horned larks will give an insight into the action of this exceedingly important factor in subspeciation.

Perhaps the best illustration of the role of environmental change is afforded by the races *insularis* and *strigata.* The close resemblance of these races has been mentioned by several authors; yet it has generally been considered that the insular race arose as an offshoot from mainland *actia* stock. The material that I have had at command does not indicate, however, that the breeding birds on the islands nearest to the mainland show any approach to *actia.* Aside from slight overlap in individual variation, it is only along a narrow strip of the coast near Santa Barbara that mainland breeding examples of *actia* show any close resemblance to *insularis,* and this might be explained by interbreeding.

The amount of the differences between *strigata* and *insularis* is, significantly, less in extent than that between *insularis* and *actia.* This suggests that *insularis* and *strigata* may have arisen from a common stock which was latterly distinct from the stock that gave rise to *actia.* Geological and paleobotanical findings pertaining to certain endemic floras in central coastal California yield supporting evidence for this theory.

Chaney and Mason (1930) have found fossil remnants of a Pleistocene forest on Santa Cruz Island. The species that comprised this forest are still living and are found today in association with each other at Fort Bragg, Mendocino County, on the northern California coast. By studying the climatic conditions where the modern association exists, it has been possible to infer those under which the Santa Cruz forest existed. The authors cited state (*op. cit.,* p. 19) : "Clearly the climate in the Santa Cruz Island region during the Pleistocene was somewhat colder and considerably more humid than it is today, and the suggestion may be made that this climate is to be correlated with that of one of the glacial epochs in the Sierra Nevada and elsewhere in North America."

One of the dominant trees in the Santa Cruz flora was *Pseudotsuga taxifolia*. On the basis of the present distribution of this tree, its ecological relationships, and its past distribution as shown by the fossil record, together with indication as to the past climatic conditions, Chaney and Mason draw certain pertinent inferences. They think that the southern limits of *Pseudotsuga taxifolia* and other northern species of the Santa Cruz Island flora were shifted southward for several hundred miles as a result of glacial climate during the Pleistocene. They further infer that the return of a warmer climate resulted in the northward restriction of these species to their present ranges of distribution. In the course of this distributional adjustment of the flora, several species established themselves in areas well to the south of the forest as a whole, and subsequent separation of the Channel Islands from the mainland has resulted in the presence on these islands of relict floras of a highly endemic nature. These inferences have a bearing on our horned lark problem.

The race *strigata* is closely bound up in its present distribution with the *Pseudotsuga* forest. Members of the race occur in the open areas in a heavily forested region where the trees are predominantly *Pseudotsuga taxifolia*. This is a northern-type forest existing in a region of considerable annual rainfall and high humidity. In other words, *strigata* exists today in scattered openings within a forest association comparable to that which existed on Santa Cruz Island and elsewhere during the Pleistocene, apparently under similar climatic conditions. We may infer that *strigata,* or rather its ancestral stock, existed along with this same type of forest in the Pleistocene, but at more southern latitudes than it occurs today. These ancestral horned larks probably had much the same associational relationships with this ancient forest as *strigata* has today in its present environment. This ancestral horned lark stock probably ranged out into the region of what is now the Santa Cruz archipelago, most of which has since been submerged. According to Chaney and Mason (*op. cit.*, p. 21), there was once a land connection: "The evidence both of the fossil elephants, and of the living and fossil plants, indicates a Pleistocene land connection for Santa Cruz Island, a connection which is entirely consistent with the structural and stratigraphic data as known from the region." That horned larks existed during the Pleistocene in that general region is indicated by a fossil record given by Miller (1929:6) for the Rancho La Brea Pleistocene deposits.

It seems reasonable to suppose that the climatic and physiographic changes that affected the distribution and speciation of the *Pseudotsuga* and the closed-cone pine forests (see Mason, 1934) also affected the distribution and speciation of the *strigata-insularis* stock of horned larks. As the Santa Cruz archipelago was formed, a part of the ancestral horned lark stock probably became isolated on the islands, evolving in the course of time into what we know as *insularis*. Another part of this ancestral stock presumably followed the northward retreat of the climate controlling the *Pseudotsuga* forest, and became restricted to the Pacific Northwest coastal area. In the course of time, with genetic change and adaptation, this stock has come to be our present *strigata*. Presumably, over the rest of its once large distributional area the ancestral stock failed to

persist. In all probability, another stock of horned larks, a stock that gave rise to *actia, ammophila,* and *rubea,* either migrated in from a distance or was present all along in the more arid interior during the Pleistocene and has since spread to the areas occupied today.

The similarity of *insularis* and *strigata,* their present distribution, the present ecological relationships of *strigata,* and the indications of past climatic conditions on Santa Cruz Island all fit in to make the hypothesis of the relationship and origin of *strigata* and *insularis* seem entirely reasonable. Climatic change and migration, physiographic change and isolation, have all apparently been involved. This method of the evolution and formation of subspecies of horned larks is essentially a splitting of an ancestral stock, with divergent and independent differentiation of the separated portions. The races *insularis* and *strigata* today possess subspecific differences, yet they retain ample evidence of near relationship. It is suggestive that the subspecific differentiation is of not earlier origin than the Pleistocene.

The fact that *strigata* today does not occupy open country in the vicinity of Fort Bragg and that *actia* does instead, is not incompatible with our theory. The race *actia* seems to have much greater limits of tolerance to varying climatic conditions than does *strigata.* The whole northern California coastal area is, in general, a wooded area, not particularly suitable for horned larks. The few places where horned larks occur in this north coast area have probably been populated by the more vigorous, aggressive *actia* stock pioneering from the southeastward. On the other hand, *strigata* seems to be a relict race with relatively few individuals and probably has not tended to expand its boundaries. *Strigata* seems to be hemmed in by barriers on all sides but the south and to have been preserved in typical form only in the extreme northern part of its range. Interbreeding with *merrilli* on its southern extension seems to be altering its genetic composition there.

One other peculiarity of the race *strigata,* which may have a bearing upon the history I have hypothesized for the race, is its migration, as testified to by at least two writers (Bowles, 1898:53; 1900:30; Burleigh, 1929:515). Members of the race, they say, move out of a region of mild winters to more southerly places. It is conceivable that this instinctive part of the racial make-up originated in the past in connection with Pleistocene climates and former distribution. There are indications of some sort of seasonal movements in the race *insularis,* too, but little is known about them.

Whether *insularis* or *strigata* is most like the ancestral stock is problematical. Possibly *strigata* is, because it occurs in an environmental situation most like that of the Pleistocene under which the ancestral stock existed. If so, it presumably would not have been subjected to as much climatic change as *insularis. Strigata* has apparently been as much isolated as *insularis,* for the Cascade and Siskiyou mountains have formed a barrier preventing any extensive contact with other races.

Strigata shares the character of yellow on the underparts only with *sierrae.* In other morphological respects these two races also are similar. *Sierrae,* furthermore, is the ecological counterpart of *strigata* in the high country of the
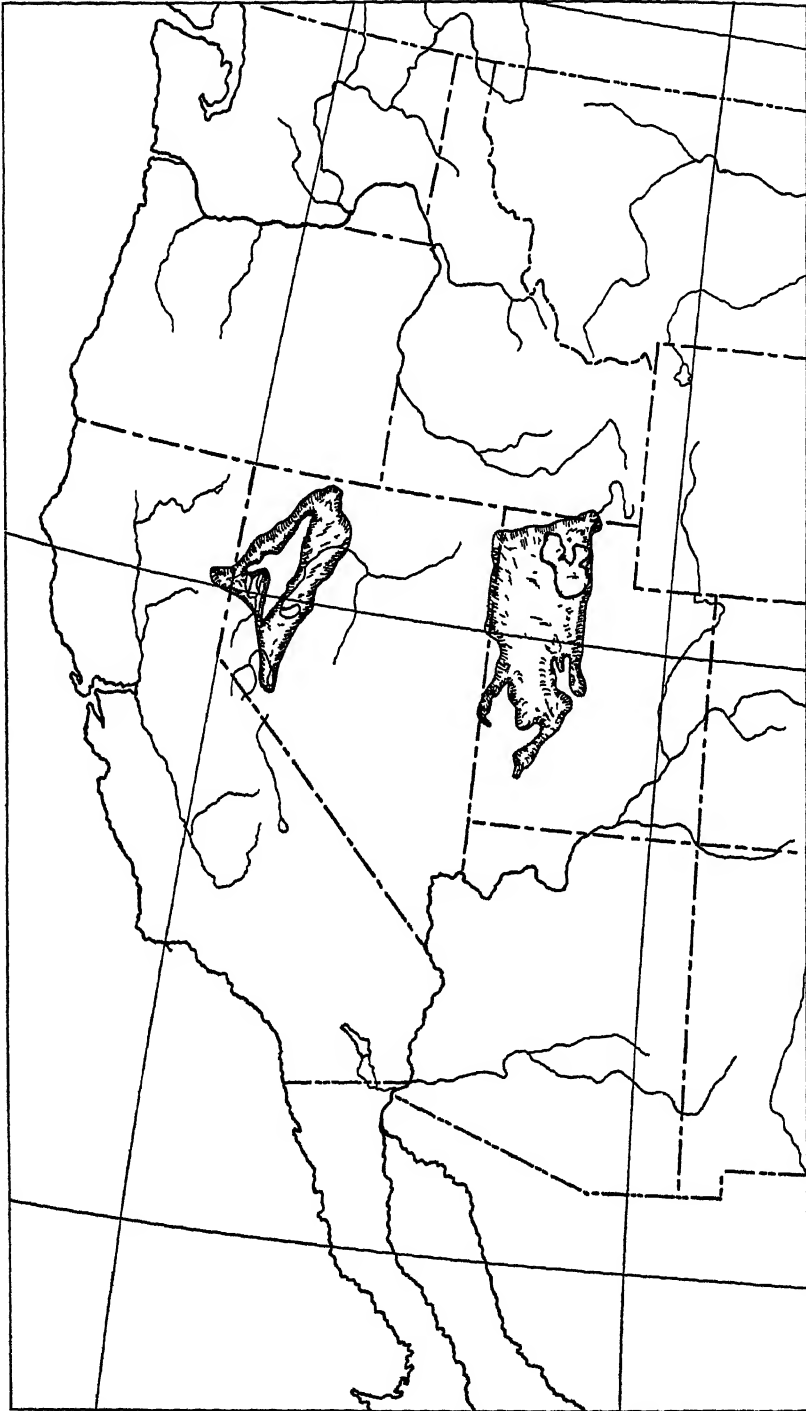
Fig. 13. Map showing in general the extent of the Pleistocene lakes Lahontan (left) and Bonneville (right). Compare these areas with the ranges outlined for the races *O. a. lamprochroma* and *O. a. utahensis* (fig. 3).

northern Sierra Nevada. It exists, we have seen, in open areas in a forested region and thus has a discontinuous distribution within its general range, as does *strigata*. Like *strigata*, individuals are probably less numerous for this reason than in races inhabiting open desert. Also, *sierrae* is relatively isolated, having little contact with other races. If we are justified in concluding that there is evidence of close relationship between *sierrae* and *strigata*, it may be presumed that *sierrae* represents another relict portion of the ancestral stock that gave rise to *strigata* and *insularis*.

We have seen one instance of how change in the external environment has been one of the underlying factors in subspeciation. Another instance is afforded in the Great Basin where we find the races *lamprochroma* and *utahensis* close to each other in their general appearances, hence in all probability only slightly differentiated. Also, the two seem to intergrade over a large area. The most striking thing about them, however, is the correspondence of their ranges, in a very general way, with the respective areas once covered by the two major Pleistocene lakes of the Great Basin, Lake Bonneville in the eastern part and Lake Lahontan in the western. This correspondence, which may be seen by comparing the accompanying maps (figs. 3 and 13), seems too close to be mere coincidence. I cannot help but think that the formation of these two races has been influenced by the history of the environmental features in these two lake beds.

Gilbert (1890) and Russell (1885), in their respective monographs on Lake Bonneville and Lake Lahontan, have shown that the two lakes existed contemporaneously during the Pleistocene in a period of general glaciation, when the climate was colder and there was considerably more precipitation than at present. Horned larks probably existed in the surrounding region during the period that the lakes were extant. With the receding of the waters and the final drying up of the lakes, horned larks from one or more stocks must have gradually pushed into the suitable habitat thus made available. In the course of time, they have come to be distributed throughout the entire area except where unfavorable conditions have prevented their existence. Judging by the general conformance of the breeding ranges of *utahensis* and *lamprochroma* with the old lake beds of Lake Bonneville and Lake Lahontan, respectively, it would seem that the formation of these races took place after the lakes dried up (since the Pleistocene) and the horned larks had spread into the areas once covered by the lakes. If so, we again have an illustration of climatic change as an underlying cause of subsequent evolution in horned larks.

Horned larks would tend to spread out and, finally, to occur all through this region because of the internal population pressures forcing individuals out into new territory and causing advance into any new area made available. This tendency can be explained on the basis of the well-known geometric rate of reproduction. Once the horned larks spread into the area made available by the climatic change and by the drying up of the Pleistocene lakes, they became subjected to the peculiar environmental influences in those separate areas. They then were molded in different directions into the differing races; that is to say, in the Lahontan and Bonneville lake areas two separate differ-

entiation centers arose. Where the two races have come together, an area of intergradation through interbreeding seems to have resulted. Or, possibly there was intermediate differentiation there. Elsewhere, the spread has continued, except as it has been checked or influenced by barriers. Thus, although the two lake areas may represent the centers of differentiation, the ranges of the present races extend beyond the areas once covered by these lakes.

Miller (1931:121) has suggested that the apparent "plasticity" involved in the formation of subspecies may be not so much a result of an inherent plasticity of genetic composition as of a lack of individual plasticity; that is to say, there is close dependence on some narrowly defined ecologic niche, which, therefore, requires the species to change in response to many minor differences in habitat whether or not a population is especially plastic genetically. Horned larks, as we have seen, are ground-dwelling. They are restricted to open country, and individuals are confined to their territories during the nesting season. Their ecologic niche is sharply defined, and they are in close contact with the substratum. These things being true, the birds would be apt to be profoundly affected by any change in their immediate environment.

Since there is environmental change and horned larks seem to be affected by it, there must be some agency that brings about concurrent change in the organism to produce continued harmony between it and its environment. This brings us to the long unanswered question of how factors in the external environment enter into the process of creating changes of an hereditary nature in the organism. The frequently observed similarity between the dorsal color tones of certain races and the soil color in their ranges leads me to believe that it is natural selection that has played, and is playing, an important role in their subspeciation.

The most conspicuous illustration of this color similarity concerns the race *rubea* in the Sacramento Valley of California. The concordance in this region between the red soil and the dorsal coloration of the horned larks is very noticeable. There is even a close correspondence between the soil color and the reddish hue of juveniles. In northwestern California in the vicinity of Alturas and Likely, where examples of the race *merrilli* are the darkest, the soil, too, as I recall, is dark. Again, in the Warner Valley of southeastern Oregon and western Nevada, the color of the soil seems to show a likeness to the dorsal tone of the race *lamprochroma*. Finally, in the Great Salt Lake region, where there is a tendency for whitish alkaline soil to prevail, we find the chalky-appearing race that I have named *utahensis*. All these areas, as well as the ranges of the other races, will bear future study to confirm or to refute the suggestion that the endemic races have all been formed through the agency of natural selection, resulting in protective resemblance to the color of the soil on which they live.

Other members of the family Alaudidae seem to show such a correspondence between dorsal coloration and ground color. The ground-dwelling crested larks of the genus *Galerida* show just as striking illustrations as do our horned larks. Meinertzhagen (1921:641) has shown a conformity between plumage colors of various races of *G. cristata* and the ground color in their respective habi-

tats. Moreau (1930) reports examples in the crested larks of the Nile Valley, where subspecific differentiation on a basis of concealing coloration has proceeded, apparently, at an extremely fast rate in response to changing color of the soil. In one instance cited, the dark hue of a race seems to have been determined by the extreme darkness of the soil on which it lives. In another, a pale race seems to have developed in conformity with a pale soil surface. By tracing the geological history of the region and the changes that have taken place, Moreau dates the origin of the dark race at no more than 10,000 years ago and that of the light one at 5000 years. These examples are somewhat similar to those in the Great Basin except that in the latter the lapse of time since the habitat became available to horned larks seems to have been longer, perhaps 25,000 years.

If we can apply the adaptive-coloration hypothesis to those horned larks in which there is a correspondence between the color of the soil and that of their dorsal surfaces, we may have an explanation of the many instances mentioned of resemblance between distant races. The probabilities are that such racial similarities are a result of differentiation in response to similar soil color. It is difficult, for instance, to conceive of *rubea* being closely or very recently related to *oaxacae*, which is located far off in southern Mexico. The resemblance of the dorsal coloration of *rubea* to the color of the soil in its environment suggests that *rubea* has been differentiated in response to that particular environmental factor. The likelihood is that *oaxacae* has also been similarly evolved and that a resemblance between the two races has thus come about merely through response of the races to a chance similarity in the environment. Such an hypothesis would also explain the great frequency of local variations within races where isolation or hybridization does not seem to be the factor involved. Other anomalous points in the distribution and differentiation of the races may also be so explained. Oberholser (1902:802) formulated the question, "Why, for instance, is the form inhabiting the San Joaquin Valley, California, not the same as the one in the Sacramento Valley, as the similar conditions of climate and topography would lead us to expect?" Now that it has developed that part of the range of *ammophila* lies also in the Great Valley, the situation is even more complicated. It seems to me that the clue to this peculiar differentiation again probably lies in differences in soil coloration.

The problem of barriers is intimately linked with the problem of limiting factors. In fact, limiting factors in themselves constitute barriers to distribution. Barriers, by preventing further distribution and mingling of stocks, constitute an important consideration in the attempt to ascertain the factors entering into the process of subspeciation of horned larks. They explain many phases of distribution.

Ordinarily, in speaking of barriers, one conjures up some mechanical or tangible barrier, such as a mountain range or body of water. But, as Grinnell (1914) has emphasized, there are important intangible barriers to be considered as well, these being zonal, faunal, and associational in nature. In our discussion of the ecological relationships of horned larks, we have noted that open country and comparatively little vegetation are, apparently, necessary

features of their environment. Consequently any area of heavy vegetational cover, be it composed of forest, or chaparral, or dense annual plant growth, will serve as an associational barrier, just as will a barren salt flat or gravelly alluvial fan, because of the absence of food and of places of refuge.

Some of the races show close limitation at boundaries of life zones, which indicates that the factor of temperature has been an important barrier in their evolution. Temperature conditions other than those within the limits of tolerance of the subspecies apparently act as barriers. For instance, the race *arcticola* is restricted today to boreal conditions by a zonal or temperature barrier. This is as effective a barrier as is a body of water. Requisite boreal conditions occur only in certain areas on separated mountain tops, and we find the colonies of this race in these places only.

The close dependence of *arcticola* on boreal conditions suggests that the race was formed under the influence of such conditions. Furthermore, in view of the earlier, more widespread prevalence of those boreal conditions, it may well be postulated that *arcticola* at one time had a correspondingly greater and more southerly distribution. If this was so, then with the retreat of the colder climate northward, *arcticola* presumably followed. McCabe (1936) has recently given such a picture of climatic change and endemism in the Northwest. If we fit the conditions as we find them in *arcticola* to the facts and inferences in his paper, this race seems to be a part of the relict fauna of the boreal conditions, just as his other examples are. From this it would seem that temperature, acting in conjunction with other environmental factors, has played an important role in the formation of the races of horned lark and in determining their present distribution.

Other instances of close adherence of different races to definite life zones are to be seen in *sierrae* in the Transition Zone of the northern Sierra Nevada, *leucansiptila* in the Lower Sonoran Zone of the Colorado Desert region, and *enertera* in the Lower Sonoran of Lower California. Yet in contrast to these examples of zonal distribution, we have races such as *actia,* each occurring in several zones, and three races in the Great Valley within the same zone, as well as two races in the Great Basin region and the great numbers of local variations which exist under the same zonal conditions. Also, in northeastern California, in Lassen County, *merrilli* and *lamprochroma* come together with only a narrow belt of intergradation; here, temperature conditions are undoubtedly the same in the intermediate area as in the immediately adjoining areas occupied by the different races. We are, then, left with the feeling that although sometimes temperature has been an important factor, it does not seem to have been critical for all races, and certainly is not the sole factor, nor even the most important one, in the evolution of some of the races.

Much the same may be said of faunal barriers that bring in the role of humidity. We have certain instances among the races here considered of fair correspondence between ranges and accepted faunal areas. Thus we find the range of *leucansiptila* coinciding very closely with the Colorado Desert faunal area of Grinnell (1915), *insularis* with the Santa Barbara Island area, *rubea* with the Sacramento Valley area, *sierrae* with the northern part of the Sierra

Nevada faunal area. In contrast, we have *ammophila,* occupying a range comprising all of the Mohave Desert area and part of the Inyo and San Joaquin areas, and *actia,* occurring in the San Diego, San Joaquin (part), Sierra Foothill (part), Santa Cruz, San Francisco Bay, and Northern Humid Coast areas.

In a general way, there is correspondence between intensity of coloration and degree of humidity. Races dwelling in the interior, arid, desert regions possess the palest colors, whereas the coastal and mountain races, which occupy more humid areas, are darker in coloration. Thus, *actia* is darker than *ammophila* and *leucansiptila; insularis* is darker than *actia; sierrae* has a darker coloration than *lamprochroma* or *utahensis.* Perhaps the brownest of all the races is *strigata,* which occupies the most humid section of the western United States. Despite these instances of correlation between dark coloration and high humidity and light coloration and low humidity, such anomalies come to light as the blackest race, *merrilli,* breeding in an area of relatively slight humidity; and again, as noted above, the occurrence of two races in the Great Basin, three in the Great Valley of California, and races like *actia,* each occurring in areas of widely varying humidity. We also have duplication of color tones in areas of differing humidity. Such examples raise the question whether the general correspondence between dark colors and areas of relatively high humidity is the result of the direct effect of humidity on the organism, or whether there has been some indirect cause, like natural selection and soil color. As with temperature, we may admit that the effect of humidity as a faunal barrier has had something to do with subspeciation, but other factors seem equally important. I am inclined, as previously stated, to place emphasis on the factor of concealing coloration and the agency of natural selection.

Turning now to the more tangible or mechanical sorts of barriers, we can point to a few instances of their presence and effectiveness. The Warner Mountains in southeastern Oregon and northeastern California seem to form an effective barrier separating, throughout their length, the races *merrilli* and *lamprochroma.* To the south and probably to the north of this range the two races come together and intergrade. Similarly, we find the crest of the Cascade Range separating the races *strigata* and *merrilli.* There is some evidence that these two races intermingle in the Columbia River region and also at the southern end of the range in Siskiyou County, California. *Lamprochroma* and *sierrae* are separated in places by mountain barriers, as are *actia* and *leucansiptila.* The water surrounding the Santa Barbara Islands forms a barrier for *insularis.* Except perhaps for the last, scrutiny brings out the fact that these seemingly "mechanical" barriers really resolve themselves into "intangible" ones—temperature, humidity, or associational limitations, any two or all of these.

Barriers to distribution prevent continued spread and intermingling of races. Interposition of barriers produces separation and isolation of populations. That isolation has played an important role in the formation of races seems a certainty, for example, when we consider *insularis* and *strigata.* At the same time, it does not seem to have had so important an influence within

races. In *insularis, arcticola,* and *sierrae* there are no local peculiarities in the isolated colonies. There are several factors, as discussed in the account of *insularis,* that may explain the varying role of isolation. Isolation may never be more than an aid in the speciation process; it is certainly most effective when there are marked differences in the environments of the isolated populations or when decided environmental changes occur simultaneously with the isolation.

That hybridization or interbreeding of populations has been an important factor in differentiation has been indicated. We have seen instances of increase in variability on the peripheries of ranges where two or more races come together. The apparent intermediates between *strigata* and *merrilli,* and between *sierrae* and *merrilli* or *lamprochroma* are suggestive of interbreeding. In almost no instance can it be ascertained whether the large intermediate populations are the result of hybridization or of differentiation by reason of an intermediate kind of environment.

Conclusions concerning subspeciation.—We have discussed several instances of differentiation in horned larks and have considered some of the factors involved. Much of the subspecific differentiation seems to have taken place since the Pleistocene, several evolutionary processes appearing to have been involved. The basic feature seems to have been climatic and physiographic change, with consequent effects on horned-lark distribution and differentiation. The suggestion has been made that, in some instances at least, adaptive change in characters has come about through the agency of natural selection working on gene mutations. Another process involved is the splitting of a geographically variable parent stock and the dropping out of spatial intermediates. This, with the aid of isolation and environmental change, has resulted in separate subspecies. There is some evidence that populations have arisen through interbreeding or hybridization of races. In this connection isolation again has probably been a factor. Barriers of temperature and humidity, as well as associational and mechanical ones, also seem to have played a leading part in subspeciation.

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WHITE-BREASTED NUTHATCH   BROWN CREEPER
BARRED WOODHEWER   DOWNY WOODPECKER

TRUNK-CLIMBING BIRDS

ADAPTIVE MODIFICATIONS FOR TREE-TRUNK FORAGING IN BIRDS

BY

FRANK RICHARDSON

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CONTENTS

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BY

FRANK RICHARDSON

(Contribution from the Museum of Vertebrate Zoölogy of the University of California)

INTRODUCTION

CORRELATION of form and function is so universal among animals, and often so obvious, that it has been known since the beginning of biological science. Not until comparatively recent time, however, have specialized structures that are correlated with functions been analyzed with respect to their mechanical aspects and the part which they may play in evolution. This paper compares the parallel structural adaptations of several groups of birds having the same habit of foraging on tree trunks. Previous workers have treated comparable parallelism in a restricted manner, often employing only the skeletal system. The chief aim here is a detailed evaluation of parallel adaptation shown in interrelated structures or organ systems.

Functional-anatomical studies may deal with just one kind of animal, but ordinarily several forms are compared. Such comparisons offer a convenient and necessary check on interpretation and disclose the evolutionary significance of the specialized structures. In general, there are two types of comparative functional-anatomical study: one of closely related forms, the other of distantly related forms. The first type leads to an understanding of the phylogeny of a well-circumscribed group or of the evolution of its adaptations. This is most often accomplished by analyzing varying degrees of the same adaptations in the related forms. Important work of this kind has been done by Burt (1930) on genera of woodpeckers, by Miller (1937) on genera of geese, and by Engels (1940) on species of thrashers. In the study of distantly related animals, one of the chief aims is to establish the validity of qualitative and obvious adaptations by showing their occurrence in unrelated species of the same habits. This is essentially a consideration of convergent or of parallel adaptation. Stolpe (1932) has written an important paper of this type on the adaptations of the hind limbs of birds for various general habits of living. Steinbacher's work (1935), correlating structure and function in the feet of birds, is significant in demonstrating that different structural types can be adapted to the same use, or that the same structural type can be adapted to several uses. Two other eminent students of convergent and parallel adaptation, largely in vertebrates other than birds, are Abel (1912), who has written on paleontology from an adaptive standpoint, and A. B. Howell (1930), whose principal work in this field is on aquatic mammals.

The present study is comparable to Stolpe's in that unrelated species, representing families from two orders of birds with similar habits, have been

selected for comparison. Unlike Stolpe's work, it is of narrower scope and less general treatment. Also, quantitative comparisons have frequently been made, in contrast to Stolpe's usually qualitative (adjectival) comparisons. Admittedly, a thorough analysis of adaptations of a species can generally best be made by comparing related species which show degrees of the same adaptations. Consequently, I do not pretend to treat exhaustively the adaptations of any one species. It has usually been necessary to select the most clearly defined adaptations for comparative analysis.

METHODS AND MATERIALS

The essential method of functional-anatomical work is the comparison of structure and normal action. Habits alone often suggest the presence of well-defined structural modifications, whereas just as often structures themselves imply habits. Two approaches to the study of adaptations are thus possible, but the integration of habit and structure can best be shown only after careful analysis of both.

Certain trunk-foraging birds, such as some of the honey-creepers (Drepanididae) and wood-hoopoes (Phoeniculidae), were not available. In the representative groups chosen, particular species were selected. This does not unduly restrict the application of the results. The adaptations discussed for *Dryobates pubescens*, for example, apply to other species of this genus and certainly to all races of this species. The following is a condensed classification of the principal types used:

ORDER **Piciformes**
   Suborder **Pici**
      Family Picidae. *Dryobates pubescens,* Downy Woodpecker.
ORDER **Passeriformes**
   Suborder **Tyranni**
      Family Dendrocolaptidae. *Dendrocolaptes certhia,* Barred Woodhewer
   Suborder **Oscines**
      Family Sittidae. *Sitta carolinensis,* White-breasted Nuthatch
      Family Certhiidae. *Certhia familiaris,* Brown Creeper
      Family Troglodytidae. *Thryomanes bewickii,* Bewick Wren.

These species were available as preserved specimens, skeletons, and skins, and could also be observed in the field. Only limited observations of Central American woodhewers were possible. Caged birds of several species have been watched with profit when the actions of such birds were obviously normal.

All adult specimens of a species have been grouped together in deriving means. This could be done because no appreciable secondary sexual differences were found, *Corvus* probably excepted. Furthermore, all measurements were put on a relative (percentage) basis by comparing the proportions within each individual. Engels (1938) has already shown that secondary sexual differences in the coot, as probably in other birds, are uniform differences in all proportions. Specimens of several races were grouped together in studying *Certhia, Thryomanes,* and *Dryobates,* but no consistent racial size differences were apparent even in separate tabulations of these races.

FEEDING AND NESTING HABITS

Brown Creeper, *Certhia familiaris*

The creeper usually climbs straight up vertical trunks, but occasionally it searches for food on branches, even though these may slope downward. Climbing is always headfirst, whether on trunks or the upper or under surfaces of branches. The tail continually serves as a prop against the tree, except for an instant during each hop, or when the bird is on a horizontal or downward-sloping limb. The pressure which is put on the tail, as when the creeper pauses on a trunk to probe for food, is indicated by the bending of the tail feathers.

Climbing is accomplished by successive hops in which the feet always move in unison. Hops sometimes follow one another so quickly that little hitching motion is visible, and the creeper almost seems to run. The head and the anterior part of the body are typically thrown upward and toward the tree trunk at the beginning of each hop. This results in a repeated ducking of the head as the bird progresses upward. The feet are widespread at all times. They thus give a firmer stance and bring the body closer to the tree. The feet, as in other passerines, are anisodactyl; digits II, III, and IV are directed forward, and digit I directed backward. In climbing, digits III and IV typically are nearly parallel and are directed somewhat laterally, probably approaching a 40° angle with the main axis of the body. The hallux usually is hidden from view, because it is directed ventrally or somewhat inwardly.

I have not seen creepers feeding on the ground, and although they conceivably may, nearly all their food must be obtained from the branches and trunks of trees. Beal (1907, p. 66) analyzed the stomach contents of seven California creepers and found the food to consist of small beetles (such as weevils), wasps, ants, bugs, a few spiders, and occasional seeds. The occurrence of these insects suggests that food is obtained from exposed surfaces and from crevices of the bark. This is confirmed by observation of the birds. Wood-boring insects are lacking from the diet, as might be expected from superficial examination of the creeper's slender and decurved bill.

Nests are typically situated behind loosened layers of bark, but are sometimes in cavities of tree trunks. These cavities are never excavated by the creep-

ers themselves. Allen (1925, p. 273) mentions that they roost by clinging in a vertical position. Presumably, the tail is used for support at this time.

White-breasted Nuthatch, *Sitta carolinensis*

The climbing ability of nuthatches is more striking than that of the other trunk-climbing species studied, because nuthatches habitually climb both up and down trunks. Progression is always headfirst. The tail feathers are not used for support, are not stiff, and are noticeably short. The ability to climb downward headfirst, when the tail can give no support, demonstrates a complete lack of need for such support.

Climbing, as in the creeper, is by modified hopping. The same ducking movement at the start of each hop can usually be seen. The feet usually are placed
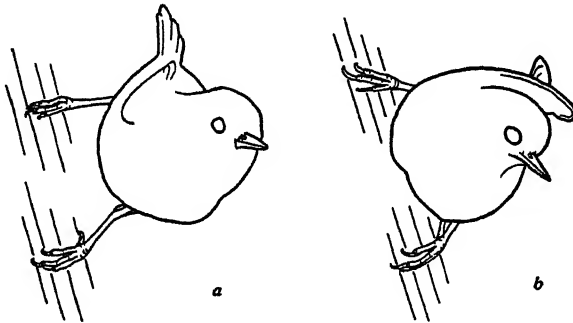
Fig. 1. Mountain chickadee (*Penthestes gambeli*), *a*, and pigmy nuthatch (*Sitta pygmaea*), *b*, clinging to side of tree trunk. Note especially the position of the feet in relation to the body, and the distance of the body from the tree trunk. Outlines traced from photographs of birds which came to the same position on the same tree.

wide apart (fig. 1) and with the line between them not at right angles to the vertical axis of the tree trunk, although at right angles to the body. Trunk-climbing birds that use the tail for support have the line between the feet approximately at right angles to the vertical axis of the tree trunk. As a consequence of the oblique stance of *Sitta*, progression is not directly vertical. The oblique position of the feet on the tree permits the bird to cling with the upper foot while it braces itself with the lower. Such action of the legs and feet is impossible when the feet are directly on either side of the vertical axis. Gravity then tends to swing the anterior part of the body outward. An oblique or even horizontal position of the body on the vertical trunk is more typical of nuthatches when they are climbing downward than upward, possibly because in going straight downward the responsibility of clinging falls entirely on the claws of the upward-directed hind toes. In climbing downward, the foot that is uppermost usually clutches the bark with the axis of the middle toe approximately at right angles to the vertical axis of the tree. Furthermore, this foot is generally well away from the body and appears to be lowering the body as well as holding it (plate 24). Many of these features of the climbing of nuthatches have been discussed and figured by Law (1929, pp. 45–51).

White breasted nuthatch (*Sitta carolinensis*) pausing while climbing downward Note especially the position of the upper foot and its toes Photograph taken at Grand Canyon, Arizona, August 30, 1938

Nuthatches obtain their food from the surface of the bark by probing cracks, or by forcefully scaling off loose bark by prying or pecking with the bill. Not infrequently, though, the bill is more vigorously used in pecking a hard article of food (such as a pine seed) wedged in the bark on the upper surface of a limb. In such pecking, the head is drawn well upward and backward at the start of each stroke, and the bill is driven directly into the food. Often the bird seems to put all the power it can summon into this drive. Nuthatches occasionally forage on the ground, especially if food is put out for them. When hopping on the ground, they have a noticeably squat position, with the body close to the ground and the feet wide apart. This stance suggests the climbing adaptations of the bird.

The stomach contents of 34 white-breasted nuthatches examined by Sanderson (1898, pp. 144–155) shows that the food of this species is 25.7 per cent insects and 67.4 per cent seeds in the winter, but 79.5 per cent insects and 13.5 per cent seeds in the summer. Boring insects are not included in the diet. The seeds eaten by this species, as shown in one study (Henshaw, 1913, p. 9), are more than half acorns or other large, hard-shelled nuts or seeds. Such food indicates much forceful pounding with the bill.

All species of nuthatches dig their own nesting cavities at times, but usually occupy ready-made holes. Most cavities which nuthatches dig are in fairly rotten wood and are often started at old woodpecker workings. Even so, this digging demands very forceful use of the bill and probably is made possible only by special structural adaptations. Grinnell (1930, pp. 323–326), in recounting observations of digging red-breasted and pigmy nuthatches, emphasizes the vigor and persistence of their work.

Bewick Wren, *Thryomanes bewickii*

The Bewick wren most often forages in bushes or on the ground, but also searches for food in trees. It climbs well on the bark of trees, but rarely forages on vertical trunks or on the under surfaces of large branches. It is an excellent climber in bushes, even clinging upside down. The feet are not held far apart. The frequent movement of the long tail when the bird is climbing among branches suggests that the tail is an important balancing organ. Flight, such as from bush to bush, is more frequent in this species than in the trunk-climbing species. When the wren is foraging in trees it explores crevices in the bark much as does a creeper. The bill is sometimes used to move accumulated leaves or twigs when the bird is foraging on the ground. Beal (1907, pp. 57–60) reports that the stomach contents of 146 Bewick wrens was 3 per cent vegetable matter, the remainder being animal matter, chiefly bugs and beetles. Wood-boring insects are not included in the diet.

Downy Woodpecker, *Dryobates pubescens*

The downy woodpecker represents the more highly specialized trunk-foraging woodpeckers. Its habits are closely similar to those of such specialized trunk-foraging species as the hairy, Nuttall, and three-toed woodpeckers. Structural comparisons of woodpeckers by Eckstorm (1901) and by Burt (1930) corrobo-

rate the conclusion derived from a consideration of habits, namely that *Dryobates* is one of the genera which is most highly adapted for trunk foraging.

The climbing of the woodpecker (see especially Stolpe, 1932, pp. 214–215) is essentially like that of the creeper, both with respect to the use of the tail and the upward hitching movement accompanied by inward ducking of the head. The foot of woodpeckers is zygodactyl, digit IV being directed either backward or to the side (fig. 2). Stolpe emphasizes the importance of the pincerlike action of the two fourth toes, when directed laterally and acting together, in holding the bird to the trunk. The fourth toe, when directed posteriorly, forms a strong grasping foot with the opposing digits II and III. This seems to be essential in helping digits II and III gain a firm purchase on the
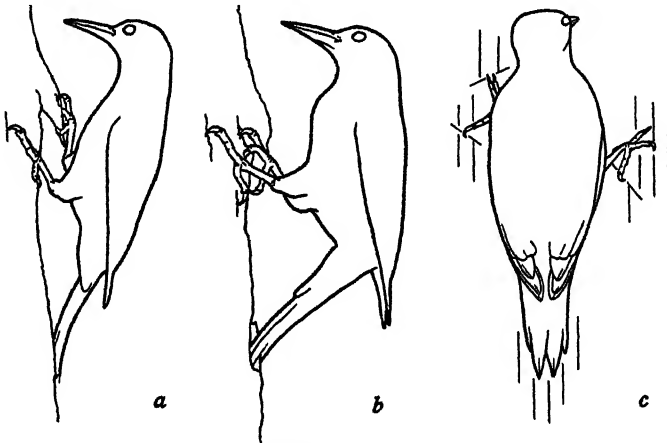
Fig. 2. Outlines of woodpeckers illustrating use of tail and feet. *a*, eastern flicker (*Colaptes auratus*) in normal position on tree trunk; *b*, flicker probably ready to spring from tree. Note how the body can be pushed from the tree by changing the angle of the tail, and that only the tips of the claws are in contact with the bark. *c*, hairy woodpecker (*Dryobates villosus*) showing widespread feet and reversed or lateral position of fourth toe. *a* and *b* traced from photographs by Irving (1920, pp. 12–13), *c*, from photograph by Joseph Dixon taken at Eagle Lake, California, June 1, 1925.

bark. This action of digit IV is all the more important since the hallux of woodpeckers is either very small or lost. The feet, as in *Certhia*, are held in a widespread position (fig. 2), although not so far apart as in *Sitta*.

All the trunk-foraging species climb most efficiently on rough bark, for the claws here find a ready purchase. The laterally spread fourth toes of woodpeckers would seem to be of particular advantage in grasping a trunk which has slight vertical corrugation only, or in grasping the smooth sides of a small limb. *Dryobates* is, in fact, the only climbing bird studied that is often seen on small trunks or vertical branches of smooth-barked trees, such as willows.

The use of the bill in drilling for food distinguishes *Dryobates*. The drilling consists of digging, frequently in hard dead wood or bark, by repeated blows from the wedge-tipped bill. Drilling is made more effective by shifting the position of the head and bill so as to change the angle of the blows. Beal's analysis (1911, pp. 18–20) of the stomach contents of 723 specimens shows that about 30 per cent of the food of this species is wood-boring insects.

At least three other habits of woodpeckers might be reflected in the structure of these birds: the digging of large holes, either for nesting or roosting; drumming on relatively hard wood by a very rapid series of blows with the bill; and habitual roosting on a vertical surface, using the tail for support.

Barred Woodhewer, *Dendrocolaptes certhia*

My observations of woodhewers are limited, but additional information on their habits was kindly provided by Mr. Alexander F. Skutch. The climbing actions of the barred woodhewer, apparently typical of woodhewers, closely resemble those of creepers and woodpeckers. The woodhewer habitually works up tree trunks and then flies down to start upward again on another trunk. Some foraging, similar to that of the creeper, is done on branches. The tail is continually used for support. The foot is anisodactyl. The basal segments of digits III and IV, as in *Sitta, Certhia,* and *Thryomanes,* are hardly separable from each other.

Woodhewers, judging from the stomach contents of 3 specimens of *Dendrocolaptes,* are almost entirely insectivorous. Like creepers, they apparently obtain food, such as ants, nonboring beetles, and spiders, from the surface of the bark or from its crevices, and from among epiphytic plants such as mosses and lichens. *Dendrocolaptes* frequently scales off bark in search for food. Probably no foraging is done on the ground. Woodhewers do not excavate their own nesting cavities. They have been seen to enter cavities at roosting time. Apparently they roost in a vertical position, using the tail for support.

Other Species Studied

Various species, other than the five just discussed, have been considered in order to test or extend conclusions. The most important of these are: the western crow, *Corvus brachyrhynchos hesperis,* a generalized passerine that forages on the ground; the red-shafted flicker, *Colaptes cafer collaris,* a relatively unspecialized woodpecker that typically forages on the ground and obtains none of its food by drilling; the northern wedgebill, *Glyphorhynchus spirurus sublestus,* a small woodhewer with a short straight bill and the habit of pounding (but probably not drilling); and the Vaux swift, *Chaetura vauxi,* a species that roosts on vertical surfaces and correspondingly has tail feathers adapted to serve for support.

SKELETAL FEATURES

The skeletal features judged to have adaptive significance may be conveniently divided into three categories: (1) bony regions modified to provide unusual strength or mechanical advantage, as for the attachment of muscles and tendons, (2) articulations which reflect degrees and kinds of movements, and (3) relative lengths of bones, usually indicating the general type of locomotion. The terminology of Howard (1929) has been used for bones and their parts.

MODIFICATION OF BONE FOR STRENGTH OR MECHANICAL ADVANTAGE

Correlations of certain features of bones with the stress and strain to which the bones are subjected may be made in any vertebrate skeleton. For example,

a large tubercle for insertion of a given muscle often reflects great strength of that muscle. Various workers, among them J. A. Howell (1917) and Koch (1917), have described such correlations. Nevertheless, more work must be done if we are to know the degree to which the configuration of bony regions is determined by muscle attachment, and the extent to which bone can be changed in ontogeny, or later, by the abnormal or excessive use of muscles. As is shown by ensuing examples, bone also can be modified as follows: for the attachment of tissues other than muscles; to provide strength in direct relation to external forces; and for the efficient transmission of force over certain points, as in the formation of sesamoid bones like the patella. Because of the close relation between them, muscles and bones may both reflect the same adaptation. This often permits two methods of quantitatively measuring a given adaptation. When both methods can be applied, a valuable check is provided.
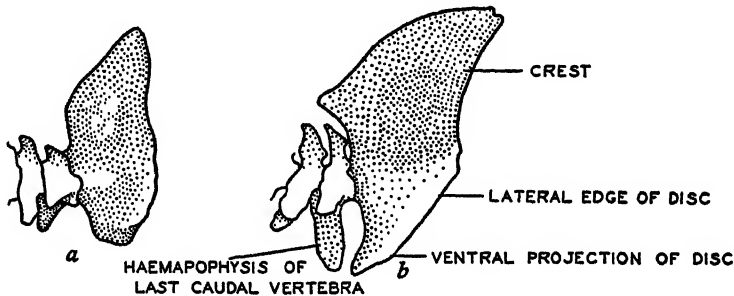
Fig. 3. Lateral views of pygostyle and two caudal vertebrae. *a, Sitta canadensis; b, Certhia familiaris;* both × 6½. Average weight of *Sitta canadensis,* 10.1 g.; *Certhia familiaris,* 7.7 g. (from 26 weights of each).

Relative size of pygostyle.—The pygostyle is intimately associated with the rectrices and the muscles which move the tail. The medial pair of rectrices is closely bound to the crest of the pygostyle (see fig. 3 for terminology). Lateral rectrices are bound to each other and, by tendinous ligaments, to the anterior margins of the disc of the pygostyle. The muscles which move the tail insert on the pygostyle or on the bases of the rectrices. The levator of the tail (M. levator coccygis) inserts chiefly on the crest of the pygostyle, whereas the depressor muscles (pubicoccygeus internus, depressor coccygis, and caudofemoralis) insert chiefly on the lateral and ventral edges of the disc.

Birds that use the tail for support when climbing have relatively larger pygostyles than other birds. Figure 3 contrasts the pygostyle of the creeper with that of the nuthatch. The length and height of the pygostyle are correlated primarily with the extent of its attachment to the medial pair of rectrices. The position of *Thryomanes* in the histograms (fig. 4) implies greater use of the tail, probably both in flight and in balance, than in *Sitta*. The projection ventrally of the disc of the pygostyle is relatively greater in the species that use the tail for support. This adds to the height of the pygostyle and, by providing a longer lever arm with which pull is exerted on the crest of the pygostyle, gives the important M. depressor coccygis a definite mechanical

advantage. The rectrices are thus more forcefully pulled downward. The width of the pygostyle, actually the greatest width of the disc, seems to be correlated with the size of certain tail-depressing muscles (chiefly the pubi-coccygeus internus) and with ligaments which bind the lateral rectrices to the pygostyle. The great width of the disc in *Dryobates* is apparently the extreme of adaptation in this direction.
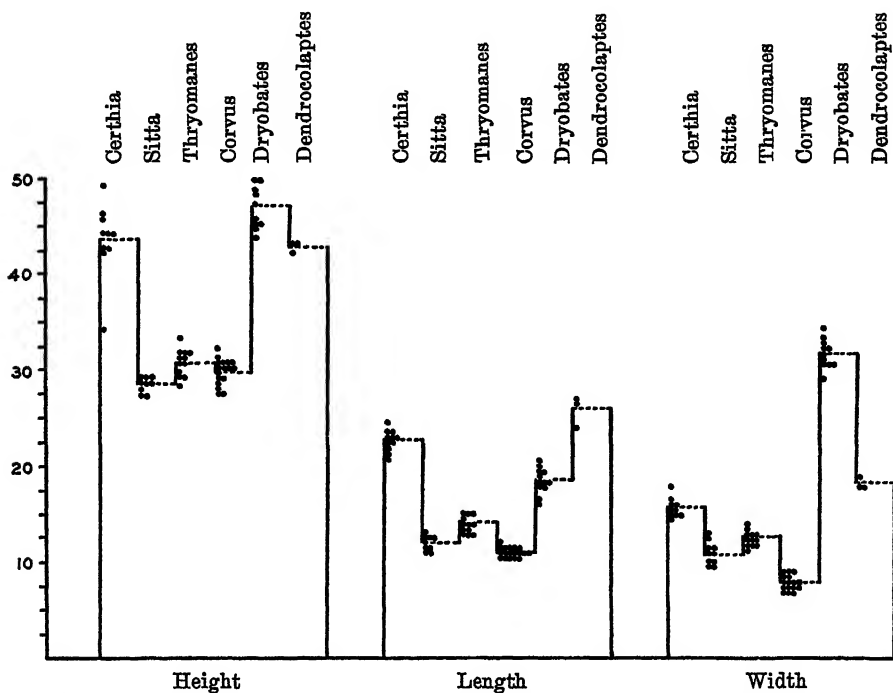

Fig. 4. Ratios in per cent of pygostyle length (anteroposterior), height, and width (of disc) to standard trunk length. Individuals on which means are based are represented by dots.

Figure 4 reveals certain constant relations between the pygostyles of the birds in question. *Sitta* has the lowest values throughout, whereas those for *Thryomanes* are consistently a little higher. All the values for these two birds are markedly lower than those of the birds that use the tail for support, among which *Dryobates* exceeds the others in two of the three values. We may there-fore tentatively conclude that the tail of *Dryobates* is the most highly adapted for support. Similarly, we may expect that the tail of *Certhia* is less adapted.

The size of the disc of the pygostyle is determined chiefly by the strength of the depressor muscles which insert on the ventral and lateral margins of the disc. Outlines of the pygostyles (fig. 5) show that birds which use the tail for support have a relatively large disc. Again, the extreme position of the nut-hatch reflects the relative unimportance of its tail. The extension ventrally of the disc is readily noticeable in birds that use the tail for support. In these the projection of the disc conceals the haemal spines of caudal vertebrae that are combined with the pygostyle.

If the complete height of the pygostyle be expressed as a percentage of trunk length, the contrast between birds that employ the tail for support and those that do not is similar to that shown by figure 5, but less. Apparently the height of the disc has changed more than has that of the entire pygostyle. It thus seems that the size and shape of the disc better reflect the use of the tail for support than does the form of the entire pygostyle.

The small differences in the relative sizes of the pygostyles of *Certhia, Dryobates,* and *Dendrocolaptes* cannot be safely interpreted in terms of adaptation. They could be caused by variations in muscular control of caudal vertebrae, body proportions, body weight, leg strength, or methods of climbing. Such
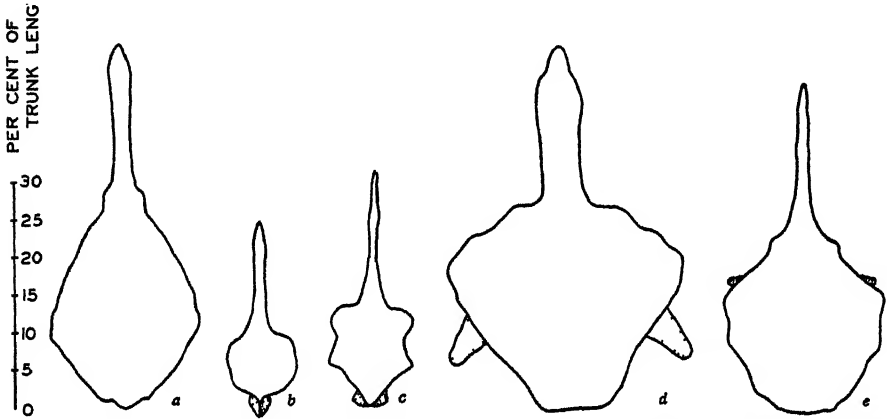
Fig. 5. Posterior views of pygostyles to show relative size. *a, Certhia familiaris; b, Sitta carolinensis; c, Thryomanes bewicku; d, Dryobates pubescens; e, Dendrocolaptes certhia.*

differences, however, do not weaken the major positive correlation of hypertrophy of the pygostyle with use of the tail in climbing.

Inclination of the disc of the pygostyle.—In birds that use the tail for support the ventral angle between the surface of the disc and the anteroposterior axis of the last two caudal vertebrae is less than 45°, whereas in other birds it is more than 70°. The inclination of the disc is determined chiefly by the articulation and bindings between the pygostyle and the last caudal vertebra. It is a measure of the degree of deflection of the rectrices, since these are bound to the sides of the crest of the pygostyle. Because of this inclination much of the disc is visible in ventral view in birds that use the tail in climbing, whereas but little is visible in the other birds (fig. 6).

Relative size of caudal vertebrae.—In ontogeny some caudal vertebrae fuse with the ilium, and a number of distal vertebrae form the pygostyle. The remaining free caudal vertebrae are of interest because they are intimately associated with many of the muscles which move the tail. Modification of these caudal vertebrae closely parallels, and further illustrates, the type of adaptation found in the pygostyle. This might be expected since the two are essentially a unit with many intrinsic muscles and bindings.

The width of the caudal vertebrae was measured between the tips of the

transverse processes. Figure 7 shows that the relative widths of the first, fourth, and sixth (last) caudal vertebrae are decidedly greater in birds that use the tail for support than in those that do not. This difference is apparently correlated chiefly with the development of the M. depressor coccygis, which originates ventrally on the transverse processes. The intermediate position of *Thryomanes*, especially in values for the fourth and sixth caudal vertebrae, will be noticed (compare *Sitta* and *Thryomanes* in fig. 6, also). This may be
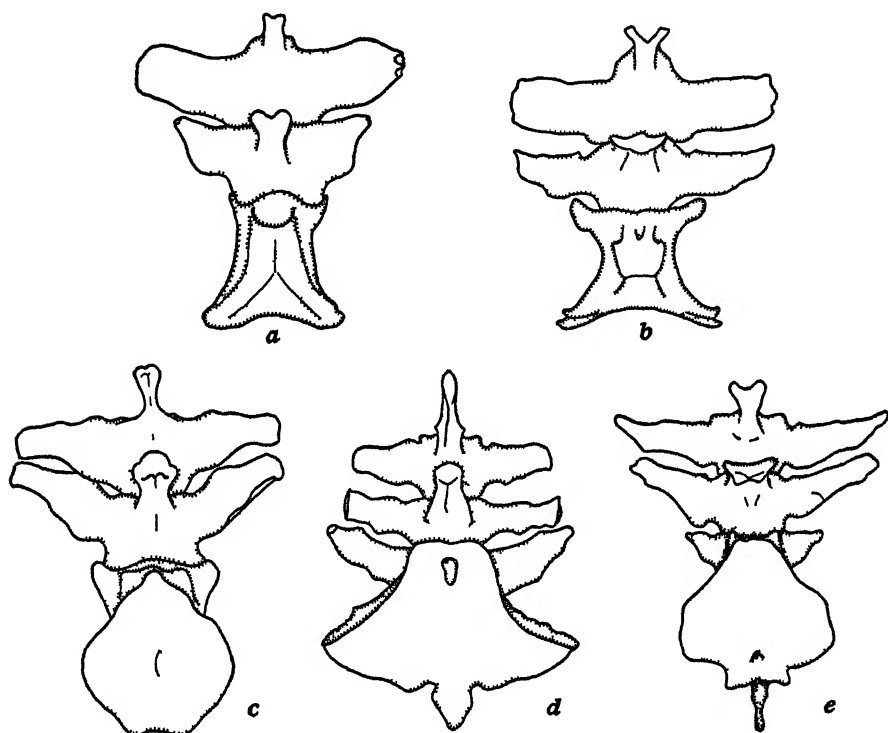
Fig. 6. Ventral views of pygostyle and last two caudal vertebrae. *a, Sitta carolinensis,* × 9.2; *b, Thryomanes bewickii,* × 9.2; *c, Certhia familiaris,* × 9.2; *d, Dryobates pubescens,* × 4.6; and *e, Dendrocolaptes certhia,* × 2.9. Note especially the expansion and antero-ventral extension of the pygostyle in the birds that use the tail for support, and the reduction of the last caudal vertebra of *Sitta.*

explained in large part by the development of the M. iliococcygeus, heads of which originate from the tips of the transverse processes of the last several caudal vertebrae. Spreading movements of the tail, accomplished chiefly by this muscle, are probably more habitual and essential in *Thryomanes* than in *Sitta* and *Certhia.* Figure 7 also bears out the tentative conclusion that *Certhia* is less adapted than *Dendrocolaptes* or *Dryobates* for using the tail for support, because it is exceeded by both of these birds in two of the measurements. The values for *Corvus* are even lower than those for *Thryomanes,* although the use of the tail is broadly comparable (in that it is not used for support) in these two birds. The similarity of *Certhia* to *Sitta* and *Thryomanes* may be explained, however, by the comparatively close phylogenetic relation of these

birds. The low values for *Corvus,* nevertheless, illustrate the contrast between birds that use the tail for support and those that do not.

The haemapophyses of the last two or three caudal vertebrae are well developed in all the species (see figs. 3 and 6). This is not surprising, because parts of the thick M. depressor coccygis insert on these processes. Owing to a greater development of this muscle, the haemapophyses are relatively much larger in birds that employ the tail for support. In general, the size of the haemal processes varies directly with that of the transverse processes. Thus,
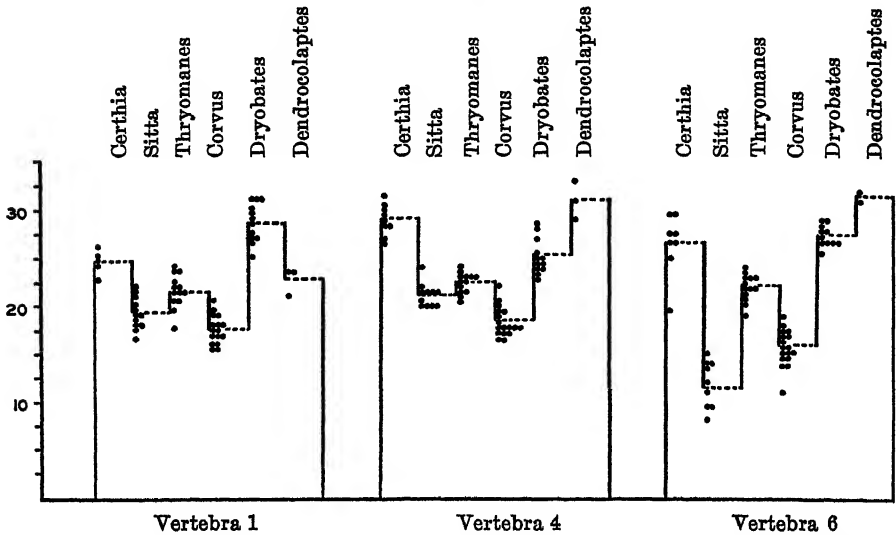
Fig. 7. Ratios of width (between tips of transverse processes) of free caudal vertebrae to trunk length. Individuals on which means are based are represented by dots.

the sixth caudal vertebra in the creeper and nuthatch is similarly proportioned in both birds, although it is relatively much larger in *Certhia.*

Relations of caudal vertebrae to pygostyle and synsacrum.—The usual number of free caudal vertebrae is 6 in each species studied, although there is variation even within a species. Variations from the usual number result from incorporation of different numbers of vertebrae into the synsacrum or into the pygostyle. For example, in one specimen of *Glyphorhynchus* the pygostyle shows no trace of a recently fused caudal vertebra, but in all three specimens of *Dendrocolaptes* and the second specimen of *Glyphorhynchus* the pygostyle clearly shows the form of a caudal vertebra fused to its anterior surface. The last caudal vertebra of the first specimen of *Glyphorhynchus* fits closely against the pygostyle and seems exactly homologous with the vertebra fused to the pygostyle in the other specimens (fig. 8). It is not clear what advantage, if any, accrues from a fusion of caudal vertebrae to the pygostyle. Even when free, the bones are so closely fitted and bound together as to act very much as a unit. Possibly fusion is incidental to great increase in the size of the haemapophysis of the last caudal vertebra, and its consequent abutment against the pygostyle.

The number of free caudal vertebrae appears to be most variable in *Certhia:* of 19 specimens studied, 12 had an additional vertebra fused to the synsacrum. This additional fusion may well be related to the development of the M. depressor coccygis, which has a large part of its origin on the posteroventral surface of the synsacrum and on the ventral surfaces of the transverse processes of the proximal caudal vertebrae. The expansion of the transverse processes of these vertebrae might result in the incorporation of an extra vertebra into the synsacrum. This should provide advantageous rigidity to the origin of
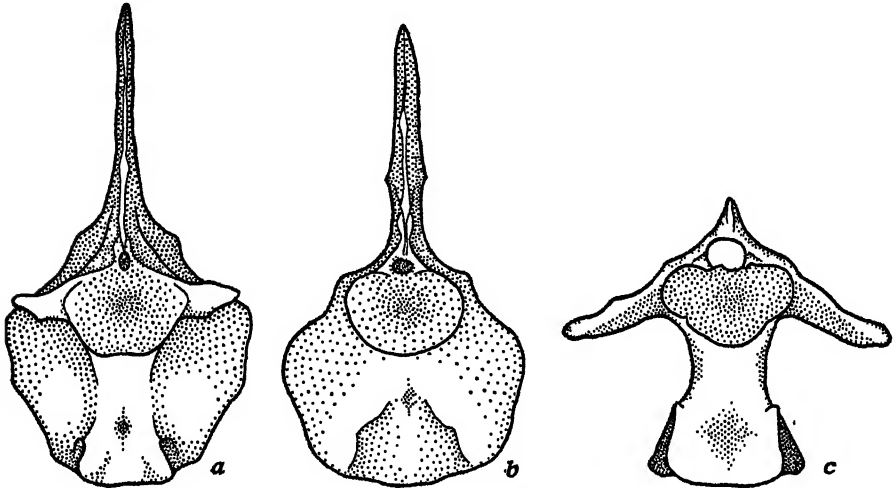
Fig. 8. Anterior views of pygostyles of *Dendrocolaptes certhia,* a, and *Glyphorhynchus spirurus* (Mus. Vert. Zoöl. no. 68740), b; c, last free caudal vertebra of this specimen of *Glyphorhynchus.* a shows fusion of caudal vertebra homologous to that shown in c. The haemapophysis of the vertebra of *Glyphorhynchus* (c) fits into the depression on the anteroventral surface of the pygostyle (b). a, × 4.5; b and c, × 9.0.

the depressor coccygis. However, the situation is confused by the fact that of these 12 birds, at least 4 had one less vertebra incorporated into the pygostyle.

Size of ungual flexor insertions.—The M. flexor hallucis longus was weighed and found to be relatively heavier in trunk-climbing birds than in nonclimbers. The M. flexor digitorum longus was not weighed, although one might expect a simliar variation in its relative size. The size of this muscle probably indicates the use of the claws better than the flexor of the hallux, because the ungual flexor of the foredigits acts more strictly on the claws alone. Hence, as shown in figure 9 (p. 330), the flexor tubercles of the foredigits have been compared. The tubercle for the insertion of the M. flexor digitorum longus is heavier and projects farther ventrally in the trunk-climbing birds than in *Thryomanes,* and is more proximally situated. This proximal location of the tubercle, and especially its increased downward projection, provides for more effective lever action of the flexor muscle, both because the lever arm is lengthened, and because the angle of the direction of muscular pull to this lever arm becomes more efficient as it approaches a right angle.

Strengthening of the skull for support in pounding.—The skulls of birds which use the bill forcefully in drilling or pecking are subjected to additional

mechanical stresses. As Burt (1930, p. 475) has pointed out in woodpeckers, the broad, straight outline of the bill reflects the necessity for an effective transmission of force. Certain features behind the bill as well reflect this necessity, and perhaps equally, the need to withstand the repercussions of such pounding. The most noticeable of these is the relative completeness of the bony interorbital septum. The lateral views of skulls (fig. 10) illustrate this point. In *Sitta* this septum is much more complete than in *Certhia* and *Thryomanes*. It is nearly complete in *Dryobates*. In the woodhewers it is somewhat more complete in *Glyphorhynchus*, whose bill is adapted for pecking, than in *Dendrocolaptes*.

Another apparently adaptive feature (shown in fig. 10) concerns the relation of the lacrimal bone to the jugal. In all the birds that use the bill for pounding (*Sitta, Dryobates,* and *Glyphorphynchus*), the lacrimal, or in *Sitta* the bone that is just anterior to the lacrimal, extends so far ventrally and lat-
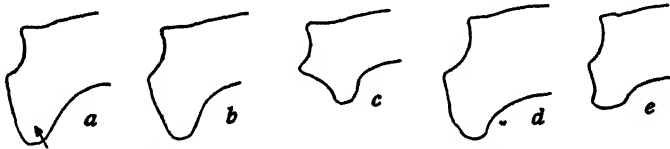
Fig. 9. Lateral views of proximal ends of the ungual phalanges of digit IV. *a, Certhia familiaris; b, Sitta carolinensis; c, Thryomanes bewickii; d, Dryobates pubescens; e, Dendrocolaptes certhia.* Note the large size and the proximal position of the tubercle for insertion of M. flexor digitorum longus (arrow) in trunk-climbing birds. Figures are on the same relative basis of per cent of trunk length. Means of phalanx measurements were derived from 5 specimens for each species except *Dendrocolaptes* (3 specimens).

erally as actually to come into contact with the jugal and be closely bound to it by connective tissue. The possible movement in the nasofrontal hinge is thus restricted, since the jugal must concomitantly move posteriorly with the action of this hinge. Any limitation of this movement of the jugal thus makes a firmer connection between the upper mandible and the posterior part of the skull. This promotes a more effective transmission of force from the skull through the bill.

Dendrocolaptes does not conform closely to the nonpecking birds, such as *Certhia,* either with respect to the interorbital septum (fig. 10) or the relation of the lacrimal to the jugal. Its lacrimal extends far laterally, and although it does not join the jugal, the two bones are bound rather firmly together (note, in fig. 10, the slight protuberance on the jugal for the attachment of bindings). These and other features of the skull or bill indicate that *Dendrocolaptes* uses the bill forcefully in prying or digging, but not in drilling.

The separate bone just anterior to the lacrimal in *Sitta* apparently is not described or clearly figured in the literature, probably because of its close relation to, and easy confusion with, the lacrimal. This bone also occurs in the Corvidae (*Corvus, Pica, Aphelocoma, Cyanocephalus, Perisoreus, Cyanocitta,* and probably others) although here it does not come into contact with the jugal or become closely bound to it. It is not present in the Paridae that were examined (*Penthestes, Baeolophus,* and *Psaltriparus*), although this family
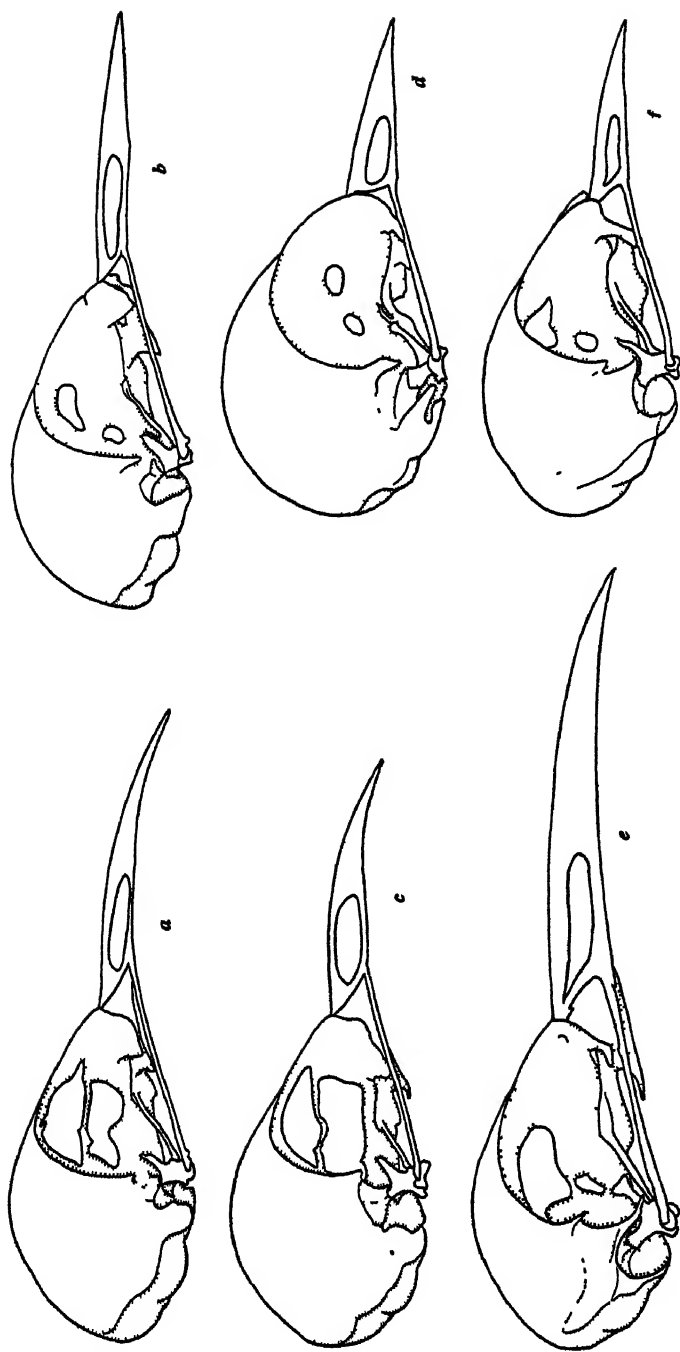
Fig. 10. Lateral views of skulls. *a*, *Certhia familiaris*; *b*, *Sitta carolinensis*; *c*, *Thryomanes bewickii*; *d*, *Dryobates pubescens*; *e*, *Dendrocolaptes certhia*; *f*, *Glyphorhynchus spururus*. Distance from anteriormost surface of lacrimal to posteriormost point of cranium is made constant in figures in order to illustrate relative lengths of bills. Posterior extent of origin of external mandibular adductor muscle indicated by dotted line in temporal fossa.

is probably closely related to the Sittidae. (It may here be reduced and indistinguishably fused to the lacrimal.) Perhaps it is present in certain fairly primitive passerines, such as corvids, but is lost in more advanced forms except, as in *Sitta*, where structural demands make it advantageous.

<div align="center">RELATIVE LENGTHS OF BONES</div>

The method used in comparing the lengths of bones of different species is important. No limb bone can be safely assumed to be of constant relative length in different species, and therefore used as a basis of comparison. In order to put such comparisons on a valid relative basis, recent workers (Böker, 1927; Palmgren, 1932; and Engels, 1938) have employed measurements along the vertebral column in the trunk region. The use of these measurements as standards of comparison seems well justified, because they involve parts of the body which appear to be little affected by adaptive changes.

Both trunk and thoracic lengths are used in the present study. The trunk length was measured from the anterior tip of the neural crest of the last cervical vertebra to the anterior edge of one of the acetabulae, instead of measuring, as did Engels, to a line connecting the two. This change aimed to increase the accuracy of the measurement, especially since small birds were being studied. The length on each side of an individual was taken and the two were compared to check the alignment of the thoracic vertebrae and sacrum. The trunk length, because of greater magnitude than the thoracic length (the inclusive ventral length of the free thoracic vertebrae and last cervical vertebra), is used in the following comparisons. In order to check the validity of these standard lengths, the relative length of the femur was calculated independently for both measurements in each specimen. The degree of shortening of the femur relative to the body was almost identical in the different species when calculated by the two methods. In comparing proportions of the skull, a different standard, termed posterior skull length, was used. This was the direct distance from the anteriormost point of the lacrimal to the posteriormost surface of the cranium. This measurement is probably stable, and was convenient to use in studying skull parts.

Trunk measurements were not complicated by variation in the number of thoracic vertebrae incorporated in the sacrum. In only one specimen (*Certhia familiaris*, Mus. Vert. Zoöl. no. 70370) was the normal number of 5 free thoracic vertebrae altered. Lengths of leg bones were measured between articular surfaces, but the small size of the phalanges made advisable the taking of the maximum lengths. The dorsal projection of the greater trochanter was used as the proximal end point of the femur. Length of claws was measured from the articulation of an ungual phalanx to the tip of its horny covering, in spite of variability in the length of the horny claw. The alternative of measuring to the tip of the ungual phalanx is inaccurate because of this bone's attenuation and consequent tendency to break when separated from its closely adhering horny claw. Furthermore, the distance to the tip of the claw constitutes the effective length of the digit, especially in trunk-climbing birds, where often only the tips of the claws catch the bark (fig. 2).

Leg-trunk ratios.—Table 1 shows the relative lengths of the leg and leg bones of the different species. The sum of the lengths of the femur, tibiotarsus, and tarsometatarsus is considered to be the effective length of the leg, because these bones together determine the distance of the bird's body from the substrate. This is in contrast to the condition in cursorial birds (Engles, 1940) or in swimming birds (Miller, 1937, p. 44), in which the toes add to the effective functional length of the leg.

TABLE 1

AVERAGE AND EXTREME LEG–TRUNK RATIOS (IN PER CENT)

Species	Number of specimens	Femur–trunk	Tibiotarsus–trunk	Tarsometatarsus–trunk	Leg (total)–trunk
Certhia familiaris....	16	75.8 (71.8–80.0)	124.2 (118.0–132.5)	106.5 (100.0–114.0)	307.0 (296.0–326.0)
Sitta carolinensis....	12	81.0 (76.0–84.5)	124.5 (118.0–129.0)	96.2 (90.0–100.0)	302.0 (285.0–312.0)
Thryomanes bewickii	12	87.5 (83.0–92.7)	152.0 (141.0–159.0)	119.0 (109.0–125.0)	359.0 (336.0–371.0)
Corvus brachyrhynchos....	17	78.9 (73.8–83.6)	131.0 (123.0–137.0)	90.8 (86.5–98.5)	300.0 (286.0–315.0)
Dryobates pubescens	12	73.4 (69.5–77.0)	108.6 (103.0–114.0)	74.2 (70.0–79.5)	256.0 (244.0–270.0)
Colaptes cafer.......	7	77.0 (75.5–79.5)	105.6 (104.0–107.0)	74.6 (72.0–76.5)	257.0 (252.0–263.0)
Dendrocolaptes certhia..........	3	72.0 (70.3–73.8)	96.7 (94.6–98.2)	76.5 (75.3–77.1)	245.0 (239.0–249.0)

Table 1 shows that *Thryomanes* has decidedly the longest legs, even in comparison with the crow (*Corvus brachyrhynchos*). This length of the legs of *Thryomanes* may be adaptive to some extent. *Certhia* and *Sitta* have legs shorter than *Thryomanes* but longer than *Dryobates* and *Dendrocolaptes*. *Dryobates* and *Dendrocolaptes* have relatively very short legs when compared to either *Thryomanes* or *Corvus*. The comparison of *Corvus* and *Dendrocolaptes* seems apt, since both birds belong to passerine families regarded as primitive or generalized. Measurements were also made of *Thamnophilus punctatus* (a member of the Formicariidae, a family which is placed in the same superfamily as the Dendrocolaptidae). The relative lengths in this species approximate those in *Corvus*. They are: femur–trunk, 85.5 per cent; tibiotarsus–trunk, 128 per cent; tarsometatarsus–trunk, 96.5 per cent; and leg–trunk, 309 per cent. The adaptive significance of shortness of the leg in trunk-climbing birds thus seems to be substantiated. Furthermore, in such branch-climbing birds as parrots and toucans the lower leg is markedly short.

On the basis of length of leg, then, *Dendrocolaptes* and *Dryobates* appear most specialized for trunk foraging. Although *Certhia* and *Sitta* have slightly longer legs than *Corvus*, they have much shorter legs than *Thryomanes*, which probably approximates their ancestral type. Possibly the creeper and nuthatch have evolved toward the short-legged condition of the woodpeckers and wood-hewers; in any case, *Certhia* and *Sitta* seem to indicate by their trunk-climbing habits that they are highly adapted and probably have modifications or habits to compensate for their relatively longer legs.

TABLE 2

AVERAGE AND EXTREME VALUES OF TOE LENGTHS EXCLUSIVE OF UNGUAL PHALANGES

(In Per Cent of Trunk Lengths)

Species	Number of specimens	Digit I Phalanx 1	Digit III Phalanges 1–3	Digit IV Phalanges 1–4
Certhia familiaris..........	15	50 5 (47.0–56.2) (16 specimens)	81.8 (77.7–87.6)	69 2 (65.2–73.5)
Sitta carolinensis..........	14	56.1 (52.4–58.3)	81.7 (76.2–85.8) (11 specimens)	62.8 (56.8–68.8) (13 specimens)
Thryomanes bewickii.......	12	46.4 (42.2–48.6)	78.0 (72.8–84.0)	56 4 (51.2–60.5) (11 specimens)
Corvus brachyrhynchos......	17	32.2 (30.9–34.8)	54.3 (51.4–58.0)	41.1 (38.4–43.6)
Dendrocolaptes certhia.....	3	24.2 (23.8–24.5)	61.3 (59.1–62.2)	64.9 (62.6–66.6)
Dryobates pubescens.......	11	20.3 (19.1–23.0)	48.3 (45.8–52.1)	56.0 (53.4–60.5)

The shortening of the tibiotarsus, as illustrated by *Certhia* and *Sitta* compared to *Thryomanes*, is probably the most significant factor in the shortening of the leg as an adaptation to trunk foraging. This would be especially true in *Sitta* where the tail is not used for support. The weight of the body of a climbing bird continually acts through the leg to pull the bird outward and downward, and to extend the joints of the leg (see Stolpe, 1932, p. 212). The leverage of this force of gravity acting to extend the intertarsal joint is decreased with the shortening of the tibiotarsus. Furthermore, such a shortening would, when the leg was strongly flexed, bring the feet farther anteriorly to an apparently more advantageous climbing position.

The general principle that distal segments of the limb are affected more than proximal segments when proportions change has been recognized in birds by both Miller (1937, p. 46) and Engels (1938, p. 212). This is also true

in the birds discussed here, except that the range in relative length of the tibiotarsus is even greater than is that of the tarsometatarsus.

Digit-trunk ratios.—The interpretation of lengths of digits is complicated because the feet of different birds are used in different ways. Also, *Dryobates* has the zygodactyl type of foot common to woodpeckers, whereas the foot of each of the others is of the anisodactyl type characteristic of passerines. Consequently, numerically corresponding toes of *Certhia, Sitta, Thryomanes,* and *Dendrocolaptes* can be compared, whereas in a comparison of these species to

TABLE 3

AVERAGE AND EXTREME VALUES OF TOE LENGTHS INCLUSIVE OF UNGUAL PHALANGES
(With Claws)

Species	Number of specimens	Digit I Phalanges 1-2	Digit III Phalanges 1-4	Digit IV Phalanges 1-5
Certhia familiaris	9	108.2 (102.0–121.9) (10 specimens)	120.4 (116.0–130.6)	107.0 (101.7–117.9)
Sitta carolinensis	12	104.0 (99.4–106.7)	116 6 (109.9–121.8) (10 specimens)	94.6 (88.3–101.0) (9 specimens)
Thryomanes bewickii	8	83.8 (79.6–86.0)	109 0 (103.1–114.2)	81.3 (78.8–84.3) (6 specimens)
Dendrocolaptes certhia	2	57.4 (54.3–60.3) (3 specimens)	84.1 (82.1–86.2)	88.2 (85.6–90.9)
Dryobates pubescens	4	38 4 (37.2–39.9)	77.0 (74.6–82.4)	86.2 (84.0–87.0)

Dryobates it is necessary to consider digits which are homologous in use rather than in number.

In tables 2 and 3 digital lengths, both exclusive and inclusive of the ungual phalanges, are compared. The shorter length is slightly more dependable because its individual variation is less. However, the major differences in complete length may be most significant, since this length is the effective functional length.

Certhia and *Sitta* always have relatively greater toe lengths than *Thryomanes,* and with one exception (digit I, phal. 1) the values for *Sitta* are markedly lower than those for *Certhia* but higher than those for *Thryomanes.* If the toe proportions of *Thryomanes* approximate those of the ancestral stock of *Sitta* and *Certhia,* the long toes of these latter birds would seem adapted to trunk-climbing. The relative toe lengths of *Corvus* are also short in comparison with those of *Sitta* and *Certhia.* This strengthens the possibility

TABLE 4
Average and Extreme Relative Lengths of Phalanges of Digits III and IV

Species	Dig. III Phal. 1	Dig. III Phal. 2	Dig. III Phal. 3	Dig. III Phal. 4 (with claw)	Dig. IV Phal. 1	Dig. IV Phal. 4	Dig. IV Phal. 5 (with claw)
Certhia familiaris........	25.8 (24.8–27.5)	26.7 (24.5–28.5)	29.0 (26.9–31.2)	39.6 (37.0–43.6)	19.4 (17.9–20.4)	21.3 (19.5–23.8)	37.4 (34.2–39.9)
Sitta carolinensis........	22.8 (21.4–23.8)	28.1 (25.6–29.8)	30.7 (29.1–32.7)	34.7 (32.4–37.7)	16.1 (14.4–17.7)	19.9 (18.2–21.3)	31.8 (29.4–34.0)
Thryomanes bewickii	24.7 (22.0–27.0)	26.3 (24.2–28.5)	26.9 (25.1–28.8)	29.8 (28.0–31.2)	15.8 (12.8–17.1)	15.7 (14.6–16.8)	23.6 (23.3–24.1)
Dendrocolaptes certhia.....	18.7 (18.0–19.3)	18.7 (18.0–19.3)	23.8 (23.0–24.7)	23 3 (23.0–23.7)	16.5 (16.1–17.1)	20.5 (19.9–21.2)	23.6 (23.0–24.3)
Dryobates pubescens........	13.2 (12.1–14.5)	15.1 (14.5–17.0)	19.5 (18.5–21.2)	28.3 (25.2–31.6)	15.1 (14.0–16.6)	15.5 (14.7–16.6)	28 9 (26.4–30.4)

that long toes have adaptive significance, although the marked shortness of the toes in *Dendrocolaptes,* and especially in *Dryobates,* precludes a general application of such an interpretation. In *Dendrocolaptes* and *Dryobates* short toes may be correlated with a more perfect modification of the tail for support.

The lengthening of the fourth toe, at least, seems advantageous even in the most specialized trunk-climbers, *Dryobates* and *Dendrocolaptes.* The fourth toe in these species is the longest and probably the most important toe in climbing. Eckstorm (1901, p. 83) discusses the length of the fourth toe in woodpeckers and points out that it generally is longest in the species that are most highly adapted for tree-trunk foraging. It is noteworthy that in both *Sitta* and *Certhia* (as compared to *Thryomanes*), the fourth toe shows a relatively greater increase in length than does the third toe.

A comparison of tables 2 and 3 reveals how greatly the ungual phalanges (with their claws) can add to the effective length of the toes. They may even double the length of the proximal phalanges (digit I of *Certhia* and *Dendrocolaptes*). Their inclusion often markedly changes comparative toe lengths. For example, in comparing *Certhia* to *Thryomanes,* phalanx 1 of the hallux is 9.3 per cent longer in *Certhia,* whereas the total length of the hallux is 29.8 per cent longer in *Certhia.*

Phalanx–trunk ratios.—Table 4 forms the basis of this discussion. All ratios are made by using trunk lengths. The numbers of specimens available are given in table 2, except those for ungual phalanges, numbers for which are in table 3.

Blechschmidt (1929, pp. 521–526) has pointed out that in general the ungual or subungual phalanges of the toes of climbing birds are longer than the basal phalanges. Miller (1937, p. 44) also, studying geese, shows distal phalanges to be most subject to change. A comparison of *Certhia* and *Sitta* with *Thryomanes* again illustrates this tendency; in each comparison the terminal phalanx (with horny claw) shows the greatest increase in length, and the subterminal phalanx the next greatest. Thus, the ungual phalanx (4) of digit III is 9.8 per cent longer in *Certhia* than in *Thryomanes;* phalanx 3 of this digit is 2.1 per cent longer; and phalanx 1 is only 1.1 per cent longer. This differential effect on distal and proximal segments is obscure or lacking in the values for *Dryobates* and *Dendrocolaptes.* In these birds the condition may even be reversed (compare digit III of *Thryomanes* and *Dryobates*). However, the phalanges of the toes of ancestral types of woodpeckers or woodhewers might disclose this same effect.

Size and shape of upper mandible.—The proportions of the bill cannot well be judged from the bony parts alone. Nevertheless, the bony upper mandible shows the length of the arc of the bill with reasonable accuracy. Figure 11 shows this arc to be greater in *Certhia* than in *Thryomanes* and *Dendrocolaptes. Certhia* and *Dendrocolaptes* have relatively the longest upper mandibles of the birds under consideration. Both length and arc are probably correlated with a probing and prying method of foraging on tree trunks. *Sitta, Dryobates,* and *Glyphorhynchus* all have straight and short upper mandibles, apparently correlated with pounding habits. The intermediate length of the

upper mandible of *Sitta* may reflect the fact that this species probes for its food as much as it pounds.

Lengths of hyoid bones.—Protrusibility of the tongue is correlated with an ability to obtain relatively inaccessible food. This is strikingly shown in many woodpeckers, a high percentage of whose food is wood-boring beetle larvae, and whose tongue is extremely protrusible. As a measure of protrusibility of the tongue, the length of the ceratobranchial and epibranchial bones of the hyoid was taken. The epibranchials of *Dryobates* form almost a complete circle, but after soaking they could be extended and measured with a tape. In the other species, where the curvature is slight and reasonably constant, the length was taken with calipers. The primary protruding muscle of the tongue, the

TABLE 5

RATIOS OF LENGTH OF HYOID BONES TO POSTERIOR SKULL LENGTH

Species	Number of specimens	Cerato-branchial	Epibranchial	Cerato-branchial + Epibranchial
Certhia familiaris....................	12	50.0	41.7	91.7
Sitta carolinensis....................	11	58.8	38.6	97.4
Thryomanes bewickii.................	7	50.0	31.9	81.9
Corvus brachyrhynchos..............	10	58.8	48.7	107.5
Dendrocolaptes certhia..............	2	50.5	33.4	83.9
Glyphorhynchus spirurus............	2	58.3	41.6	99.9 ·
Dryobates pubescens................	9	45.3	201.0	246.3

branchiomandibularis, inserts on the epibranchials. These bones are tremendously elongated in woodpeckers, correlated with their ability to protrude the tongue. As table 5 shows, no such elongation occurred in other trunk foragers. Apparently none of these species is adapted to drilling and feeding like woodpeckers, although the greater total length of hyoid bones in *Certhia* and *Sitta* as compared to *Thryomanes* may be correlated with trunk foraging.

ARTICULATIONS REFLECTING DEGREE OR KIND OF MOVEMENT

This section deals primarily with the articulations in the feet. Steinbacher (1935) has discussed and figured the feet and especially the metatarsal articulations of several groups of birds. He emphasizes that no one type of foot is adapted for one particular use. Different types of feet can be adapted to the same use (heterodactyl or zygodactyl feet for climbing) yet one type of foot can be used in different ways (zygodactyl foot of arboreal and cursorial cuckoos). This last is true of the passerines, not reported on by Steinbacher, because the structure of the anisodactyl foot of passerines is remarkably constant in spite of a variety of habits. Nevertheless, as has already been shown, there are differences in the relative lengths of digits and phalanges. Other adaptive differences are pointed out in this and the myological section.

Size of metatarsal I.—The first metatarsal of passerines and woodpeckers is the only metatarsal which remains unfused. Its digital condyle serves both

as an articular surface for the basal segment of the hallux and as a pulley for the tendon of the M. flexor hallucis longus. This tendon passes under (anterior to) the first metatarsal and over the condyle of this bone. The direction of the tendon is thus sharply changed before it continues along the ventral surface of the hallux.

The size of each drawing in figure 11 is based on the length of the first metatarsal relative to the trunk length. The metatarsal is small in *Dryobates,* as in all woodpeckers, whereas it is relatively much larger in all the passerines.
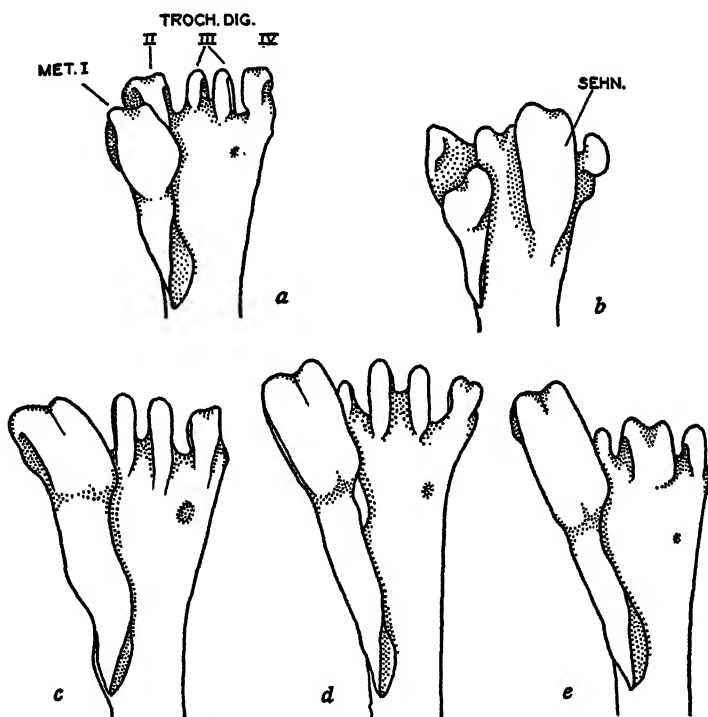
Fig. 11. Posterior views of first metatarsal and distal end of tarsometatarsus. *a, Dendrocolaptes certhia; b, Dryobates pubescens; c, Certhia familiaris; d, Sitta carolinensis; e, Thryomanes bewickii.* Size of figures based on ratio of length of metatarsal I to trunk length. Note the smallness of metatarsal I and the large *Sehnenhalter* (Sehn.) for digit IV in *Dryobates.*

The hallucal lengths given in table 3 correspond to these size differences of the first metatarsal. *Dryobates,* for example, has by far the shortest hallux. Hallucal length is no exact criterion of the development of the first metatarsal in the passerines, however, for the metatarsal of *Thryomanes* is about the same size as that of *Sitta* or *Certhia,* although the hallux of *Thryomanes* is decidedly shorter. The smallness of the first metatarsal and hallux of *Dendrocolaptes* is puzzling, especially since this bird has the typical passerine anisodactyl foot. Reduction of the hallux and its metatarsal, regardless of foot type, may be coincident with high specialization of the foredigits and especially of the tail for trunk-climbing. The long first metatarsal of *Certhia* suggests a dependence on the hallux in climbing, and less dependence on the tail for support. The tail of *Certhia* is not, in fact, highly adapted for support.

Metatarsal-phalangeal articulations.—Although the passerines show marked differences in these articulations (as the distal projection of the flanges of the trochlea for digit III), the differences were not determined to be adaptive. A striking modification in woodpeckers is the development of a large bony protuberance just posterior to the base of the fourth toe. This protuberance, the *Wendehöcker* or *Sehnenhalter* of German writers, is associated with the reversibility of digit IV. It serves as the chief articulation for the basal phalanx of digit IV in the reversed position, and as a pulley to reverse the direction of pull of the long flexor tendons of this digit (see Scharnke, 1930, p. 312, fig. 3; and Steinbacher, 1935, p. 264, figs. 25 and 26). No trace of reversibility was seen in the fourth digits of the passerines. Their basal phalanges articulate with trochlea 4 of the tarsometatarsus and also with the lateral surface of the base of phalanx 1 of digit III. The base of the fourth toe, because it is so closely bound to the base of the third, cannot be appreciably abducted.

Interphalangeal articulations.—The ability to hold the fourth toe in a reversed, or even a somewhat lateral position, is apparently of advantage to trunk-climbing birds, since it permits more secure grasp and an opposing action of the two laterally directed toes. In passerines the interphalangeal articulations typically connect the phalanges in straight lines and allow only extension and flexion between them. In trunk-climbing passerines, however, significant variation from this general condition was found in the joint between phalanges 1 and 2 of digit IV. The form of this articulation here changes the axis of digit IV so that its distal phalanges are automatically directed somewhat laterally. The action of the long flexor tendon, because of this angle in the digit, must concomitantly tend to abduct these distal phalanges.

To obtain a measure of the lateral deflection of the fourth toe, a reading was taken of the lateral angle made by the intersection of the axis of phalanx 1 of digit IV and a line across the distal edges of its condyles. Results are based on 5 specimens of each species except *Dendrocolaptes*, of which only 3 were available. The angle averaged 73°, 75°, and 80° in *Certhia*, *Dendrocolaptes*, and *Sitta*, respectively; but 86° in *Dryobates* and 83° in *Thryomanes*. The distal part of the fourth digit is thus directed more laterally in trunk-climbing birds. This adaptive trend appears to find its complete expression in the reversed fourth toe of the woodpecker. It should be remembered, though, that the reversed fourth toe of woodpeckers is probably a preadaptation (as Engels uses the term) because this same zygodactyl type of foot occurs in all picoideans, many of which are not trunk-climbers. Furthermore, certain methods of climbing, such as the oblique type of *Sitta*, and a strong development of the hallux, may make unnecessary any reversibility of the fourth toe.

Articulations between long bones of the hind limb.—Articulations between the long bones of the hind limb were not analyzed. No differences in types of movement of the legs were observed in the field. Furthermore, no means was known of determining exactly the extent of a particular movement, such as a rotation of the tibiotarsus about its long axis, in a living bird. Stolpe (1932) has made important generalizations on the mechanics of movement in the

leg joints of many types of birds, but has rarely quantitatively studied the differences. He mentions (p. 209) that freedom of movement, especially rotation, is great in the leg joints of Oscines, and correlates this with their climbing ability. This is equally true in the woodpeckers, in which Stolpe (p. 214) judges that a strong outward rotation of the anterior surface of the tibiotarsus is essential. The feet are thus thrown laterally and the body can come closer to the tree.

The knee joints of fresh specimens of *Sitta* and *Certhia*, as well as of *Dryobates*, allow relatively great outward rotation of the tibiotarsus. This is reflected by the widespread position of the feet in trunk-climbing species. Also, this outward rotation of the tibiotarsus brings the foot to a diagonal position on the trunk of the tree. The fourth digit of the woodpecker or the hallux of *Certhia* and *Sitta*, is thus brought to a posteromedial position, so that the foot is better able to grasp the vertical corrugations of the bark.

Scharnke (1930, p. 316) emphasizes the necessity of strong inward rotation of the tarsometatarsus of *Dryobates major* to bring digit IV to an effective posterolateral position. Steinbacher (1935, p. 263) disagrees with Scharnke, and shows that digit IV can be brought to this position by its own action. Steinbacher is right, although some lateral displacement of digit IV can be caused by the outward rotation of the tibiotarsus when the tarsometatarsus is sharply flexed.

Nasofrontal hinge.—Any movement of the upper mandible independent of the skull is accompanied by movement in the nasofrontal hinge. Such action has been well described by Lakjer (1926), Engels (1940), and other workers. It is made possible by the sliding of the palatopterygoid region along the sphenoidal rostrum. Movement posteriorly, with the resulting downward movement of the tip of the upper mandible, can be caused by contraction of the M. pterygoideus. A movement in the nasofrontal hinge caused by external pressure on the bill can also cause a sliding along the sphenoidal rostrum. Limitation of movement in the nasofrontal hinge may take place in various ways, as, for example, by binding of the jugal to the lacrimal, or, as was described by Engels in certain thrashers, by hypertrophy of the retractor palatine part of the M. pterygoideus. This hypertrophy seems to be correlated with the need to keep the bill from bending too far upward when, as in digging, it is being retracted against pressure.

The approximate straightness of the nasofrontal hinge of most birds does not limit the movement in the hinge. In woodpeckers (Burt, 1930, p. 475) there is a posterior incurving of this hinge and a concomitant folding over of the frontals on the nasal bones. A similar folding over of the frontals has been described by Engels (1940) in certain relatively straight-billed thrashers that use the bill in forceful blows. A similar, although less marked, folding occurs in *Glyphorhynchus*, accompanied by a slight incurving. Apparently, the folding over of the frontals is part of the telescoping of the skull correlated with pounding. The posterior incurving seems to result from a differential movement of bony parts. The sides of the hinge move posteriorly the least, apparently because they are impeded by the lacrimals at the anterior rims of

the orbit. In *Sitta,* the nasals project posterodorsally on the sides and there is a medial incurving of the hinge which gives it a wide **W** shape. This type of hinge must effectively limit movement of the bill and help make it an efficient pounding organ.

The width between the dorsolateral tips of the lacrimals was taken as a measure of the width of the nasofrontal hinge. Actually, the lacrimals extend slightly more laterally than do the sides of the hinge, but the width could be taken more accurately to the lacrimal tips because they are exposed. This measurement closely approximates the width of the base of the bill. Burt has described an increase in this basal width in woodpeckers that are highly adapted for drilling. A parallel occurs in the present study. The hinge width in *Sitta* is 36.6 per cent of the posterior skull length, whereas it is 27.9 per cent and 28.3 per cent in *Certhia* and *Thryomanes,* respectively. The width is 47 per cent in *Dryobates.* It is 54 per cent in *Dendrocolaptes,* apparently because the bill of this species, although not used for pounding, is exceptionally long and powerful.

MYOLOGICAL FEATURES

The muscular systems of the passerines studied are qualitatively uniform. Less obvious quantitative differences have consequently been sought. The quantitative analysis of muscles is frequently complicated by uncertainty with respect to the exact action of a muscle, and the difficulty of accurately measuring muscles. Nevertheless, the value of this method has been clearly shown (see Miller, 1937, pp. 19–39).

Questions of muscle nomenclature or homology are not dealt with in this paper. A. B. Howell (1938) has done the most recent and probably the most authoritative work on the homologies of avian thigh muscles, and his nomenclature for these muscles is used. The names designated by Hudson (1937), who chiefly follows Gadow, are used for the muscles of the lower leg. Gadow (1891) is followed in naming other muscles except those of the jaw, where Lakjer's (1926) nomenclature is used.

Relative Weights and Actions of Muscles of the Hind Limb

The muscles studied (see fig. 12) quantitatively are compared on the basis of their weights because it was impracticable to measure muscle volumes in small birds. Muscles to be weighed were dissected out, adhering connective tissue and in certain muscles a standard length of tendon removed, and the muscles kept in alcohol for several weeks. Weights were taken one minute after the muscles were removed from the alcohol, on a balance accurate to 0.1 milligram. The superficial alcohol on the muscles was absorbed at the outset by rolling the muscles on a paper towel. (Palmgren, 1932, p. 95, used essentially this method in weighing small muscles.) Each muscle was reweighed after an interval of several days. The two weighings never differed more than 4 per cent of the average weight. Averages of the two weighings were used in calculations. *Dendrocolaptes* is not included in the study of muscle weights because its available body weights were not dependable.

The difficulty of determining the individual actions of muscles has been

emphasized by previous workers (A. B. Howell, 1925, pp. 173–216). Interpretations of actions on the basis of dissections are valid, however, when only one muscle can perform a certain action, or when sizes of muscles can be adequately correlated with living habits. The following interpretations aim to conform to these limitations.
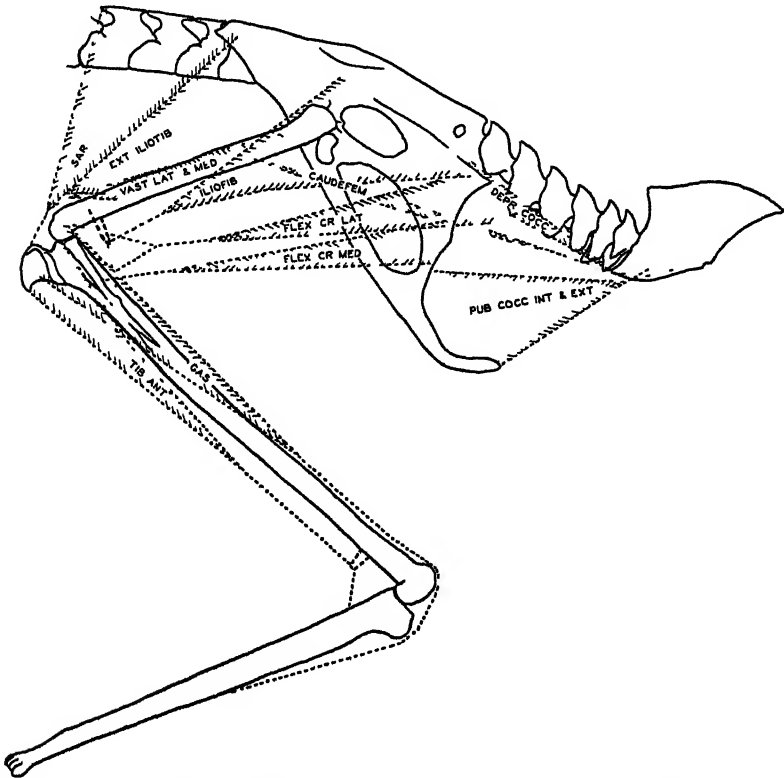

Fig. 12.—Certain muscles of the tail and hind limb. The figure is based on *Certhia*, although conditions are essentially the same in other passerines and in woodpeckers. Abbreviations indicate these muscles: caudofemoralis, depressor coccygis, extensor iliotibialis, flexor cruris lateralis (semitendinosus), flexor cruris medialis (semimembranosus), gastrocnemius, iliofibularis (biceps), pubicoccygeus internus and pubicoccygeus externus, sartorius, tibialis anterior, vastus lateralis and vastus medialis.

Extensors of the tibiotarsus.—Only four muscles can act as extensors of the tibiotarsus in birds: the vastus lateralis, vastus medialis, extensor iliotibialis, and sartorius (fig. 12). The first three of these form more or less of a unit in that they are bound rather closely together and have a common insertion on the tibia through the patellar tendon. These three muscles can be taken to represent the power to extend the shank, since the sartorius can act purely as a flexor of the femur when the tibiotarsus is held fixed. Their combined weights are compared in figure 13a. *Thryomanes* is seen to have a much greater value than have the trunk-foraging birds. This seems well explained in that *Thryomanes* is habitually in an upright position and its extensor muscles must be in nearly continual use to counteract the tendency of gravity to flex

the joints. The force of gravity on a bird on a vertical trunk, however, must be counteracted chiefly by flexor muscles (see Stolpe, 1932, p. 212). The especially low position of *Certhia* in the histogram suggests a great restriction of this bird to tree trunks.

In *Certhia* and *Sitta* the origin of the sartorius extends farther anteriorly than it does in *Thryomanes*. This origin usually extends to the anterior end of the neural spine of thoracic vertebra 3 in *Certhia*, 4 in *Sitta*, and 5 in *Thryomanes*. Probably this is an adaptation for trunk climbing, because the pulling of the body toward the tree, when the femur and tibiotarsus are held fixed, is judged to be an important action of the sartorius. The more anterior the origin (here the effective insertion) of the sartorius, the greater is the lever arm of the force pulling the body inward. Palmgren (1932, pp. 99–100) has pointed out a similar variation in the origin of the sartorius and its probable adaptive value in *Parus atricapillus*.

Flexors of the tibiotarsus.—The muscles which flex the tibiotarsus, the flexor cruris medialis, flexor cruris lateralis, and iliofibularis, are better developed in *Thryomanes* than in trunk-foraging birds (see fig. 13 *b* and *c*). The flexing action of gravity on the knee of a climbing bird apparently makes strong tibiotarsal flexors unnecessary. The use of these muscles must be frequently stressed in a bird such as *Thryomanes*, which actively feeds in various positions, even upside down, and does much hopping. However, there is at least one difference in point of insertion, and consequent lever action, which enables these muscles to act with greater mechanical advantage in trunk-climbing birds (fig. 14).

Extensor of the tarsometatarsus.—The gastrocnemius is the only muscle which acts solely in the extension of the tarsometatarsus, although the toe flexors can secondarily act in this capacity. Figure 13*d* shows the much greater development of the gastrocnemius in *Thryomanes* than in trunk-climbing birds. The reason for this seems to be exactly that which applied to the extensors of the tibiotarsus. The intermediate position of *Sitta* compared to *Certhia* (or *Dryobates*) and *Thryomanes* may reflect the occasional ground-feeding habits of this bird.

Flexor of the tarsometatarsus.—The M. tibialis anterior is the only flexor of the lower leg. *Thryomanes* has the lowest value for the relative weight of this muscle (fig. 13*c*). The almost equally low value of *Certhia* is puzzling, but the activities of *Thryomanes* may require frequent use of this flexor. Furthermore, differences in insertion give the tibialis anterior added power in trunk-climbing birds as compared to *Thryomanes*. The very high value for the tibialis anterior in *Sitta* probably reflects the fact that this bird's tail is not used for support.

Flexor of the hallux.—The M. flexor hallucis longus is the only flexor of the hallux, flexing the digit as a whole but especially the claw. Significantly, *Sitta* has the highest value for this muscle (fig. 13*f*), because this species alone depends entirely on its feet in climbing. Apparently, so strong a grasp on the trunk is not essential in trunk-climbing birds in which the tail gives added support.

Lever action of M. iliofibularis and M. tibialis anterior.—The iliofibularis originates on the ilium and inserts on the fibula after passing through a tendinous loop near the distal end of the femur. Its action is variable because the femur may or may not be held fixed by other muscles. We can assume, though, that it is a very important flexor of the shank, and that it is essential in hopping (hitching) upward, or in drawing the body toward a vertical trunk. The latter action would be true in species that use the tail for support, but
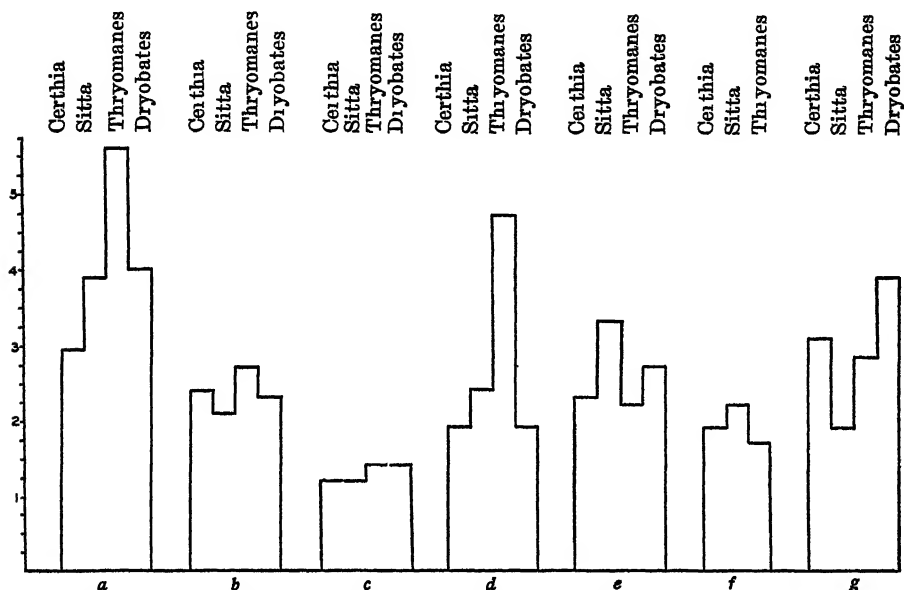
Fig. 13. Relative development of leg and tail muscles. Means represent muscle weights (4 specimens of each species) as per cent of average body weight (25 specimens of each species). The muscles represented are: *a*, extensor iliotibialis, vastus lateralis, and vastus medialis; *b*, flexor cruris medialis and flexor cruris lateralis; *c*, iliofibularis; *d*, gastrocnemius; *e*, tibialis anterior; *f*, flexor hallucis longus (*Dryobates* excluded) and *g*, tail depressors.

true in *Sitta* only when the body was oblique or lateral on the trunk. The relative length of the tendinous loop (fig. 14) varies 19 per cent of the maximum relative loop length. No functional reason for this variation is apparent, for trunk-climbing birds are not segregated from others. However, the insertion points of the iliofibularis (measured from the external articular surface of the head of the tibia to the distal edge of the tuberculum of insertion of the muscle) show a marked and apparently adaptive segregation of these birds. The insertions in trunk climbers are more distal on the fibula than those in nonclimbing birds (*Thryomanes* and *Corvus*). The range of variation is 30 per cent of the maximum relative distance from the insertion of the iliofibularis to the head of the tibia. If this distance from the insertion to the head of the tibia (the power arm) is increased in relation to the length of the tibiotarsus (the weight arm of the lever system), the force which the iliofibularis can exert also increases.

Figure 14 illustrates adaptation in the M. tibialis anterior similar to that

just described for the M. iliofibularis. The power arm of the tibialis anterior
was measured from the articulation on the head of the tarsometatarsus to the
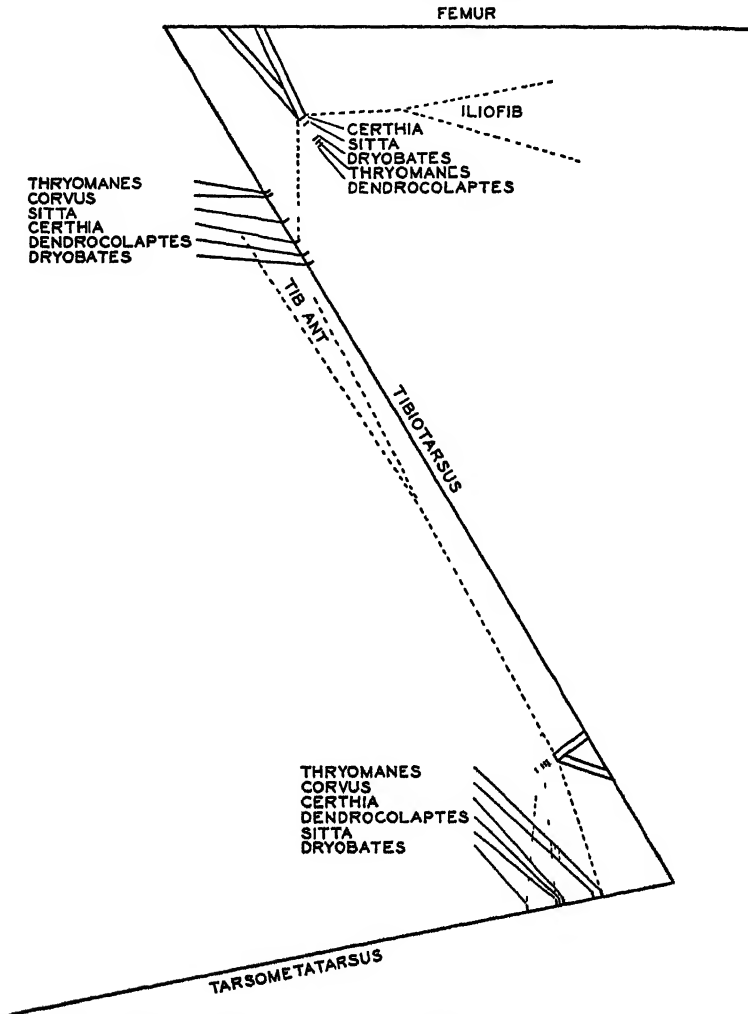insertion point of the muscle. The range of variation of this distance, based

Fig. 14. Lever systems of M. iliofibularis and M. tibialis anterior. The tendon of the
iliofibularis passes through a tendinous loop near the end of the femur. The tendon of the
tibialis anterior passes through the loop of the ligamentum transversum near the end of
the tibiotarsus. All insertions and loop lengths are plotted on the same scale: loop lengths
in per cent of trunk lengths; points of insertion (as distances to first proximal articulation)
in per cent of tibiotarsal or tarsometatarsal lengths. Long bone lengths of the diagram are
those of *Corvus*. Number of specimens: 4 of each species for loop lengths and 10 of each
species for insertions, except *Dendrocolaptes* (3 specimens).

on tarsometatarsal length, is 51 per cent of the maximum distance. Trunk-
climbing birds, again, have the longest power arms and hence the greatest
power per unit of contraction in the tibialis anterior. A concomitant modi-
fication is found in the ligamentum transversum loop, through which the
tendon of this muscle passes. The length of this loop, measured as the vertical

distance from its outermost point to the surface of the tibiotarsus, increases in the several birds in exactly the same order as the power arms. The range in relative loop lengths is 39 per cent of the maximum length.

Palmgren (1932, p. 101) similarly analyzes the action of the tibialis anterior in *Regulus regulus* and *Parus atricapillus* and indirectly shows the mechanical advantage of an increased relative distance of the insertion from the intertarsal joint. Stolpe (1932, p. 213) mentions the lengthening of the ligamentum transversum loop in woodpeckers, although he apparently overlooks the greater change in the insertion point of the tibialis anterior. He points out that this muscle acts with greater efficiency because of the lengthening of the loop. The pull of the tendon is thus more nearly vertical to the tarsometatarsus. He also believes that the longer loop enables a more efficient transmission of muscular force when the tarsometatarsus is strongly flexed, as it is in a trunk-climbing bird. This seems likely in that friction between the tendon of the tibialis anterior and the loop would diminish with a decrease of the angle made in the tendon by the loop. These adaptive features of the ligamentum transversum apply to the several trunk-climbing birds of this study.

Tendons and Bands of the Feet

Differences in the tendons of the feet are mostly quantitative, owing to the general uniformity of passerines. *Dryobates* again stands apart because of its zygodactyl feet and the attendant differences in tendons and muscles. Most of its qualitative differences, however, do not seem to be adaptive for trunk climbing. A few descriptive features of the feet are pointed out, but more description is unnecessary, as the feet of representative woodpeckers and passerines have been well described by Steinbacher (1935, pp. 262–268) and Hudson (1937, figs. 1–17 especially). Discussion is here based on dissection of both feet in at least two specimens of each species.

Insertions of toe flexors.—Only slight differences were noticed in the insertion of toe flexors, and these were not always constant. One difference from Hudson's description of the crow (see his figs. 2–4) was noted in all the birds: the proximal insertion of the M. flexor perforans et perforatus digiti III was almost entirely on the proximal end of phalanx 3 rather than strongly on the distal end of phalanx 2. Also, the proximal insertion of the M. flexor perforatus digiti IV was always either partly or mostly on the proximal end of phalanx 2 rather than only distally on phalanx 1.

The insertion of the M. flexor perforatus digiti IV on the proximal end of phalanx 3 is noticeably much stronger on the lateral side than on the medial side in the creeper and woodhewer as compared to the wren and nuthatch. The articulation between phalanges 1 and 2 of digit IV similarly indicates a greater ability of the former birds to abduct the distal segments of the fourth toe, because the joints in these two birds allow decidedly the greatest outward turning (p. 340).

Special devices: ligaments and bands.—The M. flexor digitorum longus and M. flexor hallucis longus of all the species give off fibroelastic branches to the ventral regions of the joints between terminal and subterminal phalanges.

Hudson (1937, pp. 47 and 49) describes such bands in the crow. They were originally described and figured by Schaffer (1903, p. 380, fig. 1). Hudson considers these fibroelastic bands as true insertions of muscles, but this does not seem correct, because their elasticity must preclude any tendonlike transmission of force. Possibly they function to keep the long flexor tendons in place. Additional fibroelastic bands, apparently not heretofore described, were in all the passerines studied. These bands diverge from the tendons of the M. flexor digitorum longus, one band going to the region of the joint between phalanges 3 and 4 of digit IV and the other to the joint between phalanges 2 and 3 of digit III. These, as well as the distal bands, may represent true tendinous insertions of ancestral forms. This is suggested by the fact that the bands are continuous with integral parts of the flexor tendons.

An elastic band (fig. 15*b*) passing from the dorsodistal surface of the subterminal phalanx to the dorsoproximal edge of the ungual phalanx was found in several species. Hudson (1937, p. 51, and fig. 17) has described such an automatic extensor for the claw of the hallux in the crow and the raven. The device has been previously described by Schaffer (1903, p. 380, and fig. 1) and Kopperi (1928, p. 190). Its presence apparently is correlated with the extreme reduction, probably to a functionless state in passerines, of the M. extensor hallucis longus. Such an extensor band is well developed in *Thryomanes* and *Dryobates*. In *Dendrocolaptes, Certhia,* and *Sitta,* it is less developed, and, although containing a reduced amount of the same tissue, is usually inelastic. In these last three birds, however, well-developed tendons or ligaments, automatically extend the claw of the hallux. No elastic extensor bands were found on the foretoes, except for small but very elastic bands in *Dryobates.* The lack of such bands in the passerines seems correlated with the fact that the M. extensor digitorum longus, which extends the ungual phalanges, is well developed. The comparable development of this muscle in *Dryobates* suggests that elastic bands are here adaptive in affording more perfect control of the claws.

An ability strongly to extend the claw of the hallux is probably essential to trunk-climbing passerines because the hold of this claw must be completely loosed before the bird can hop upward. Elastic extensor bands are probably efficient but not strong extensors of the claws. However, in the passerines studied a pair of ligaments apparently acts as an automatic extensor of the hallux claw. Although these inelastic bands are not associated with muscles, they are like tendons in appearance and strength. The extensor device they form was not found mentioned in the literature. The medial ligament "originates" from the first metatarsal and the bases of digits I, II, and II (fig. 15). The lateral ligament, only partly shown, "originates" from binding tissues at the ventrolateral region of the base of the hallux, and also from the medial ligament where it crosses the ventroproximal part of the hallux. These ligaments are in all the passerines studied, but their "origins" vary somewhat between species. In *Sitta,* for instance, the lateral band has a definite attachment to the base of digit II, whereas the medial has no definite attachment to digit II. In *Dendrocolaptes,* and also in *Xiphorhynchus,* the whole median

ligament is missing. The lateral ligament here "originates" only from the proximolateral surface of the hallux and is joined near its "origin" by the small tendon of the M. flexor hallucis longus.

Apparently, only extension of the foretoes, especially of digits II and III, enables the automatic extensor ligaments to elevate the claw of the hallux. The perching bird, whether on a horizontal or a vertical perch, has the bases of the foretoes in a flexed position. When the bird leaves this perch, whether to hitch up a trunk or to fly, the foretoes are extended by the action of the M.
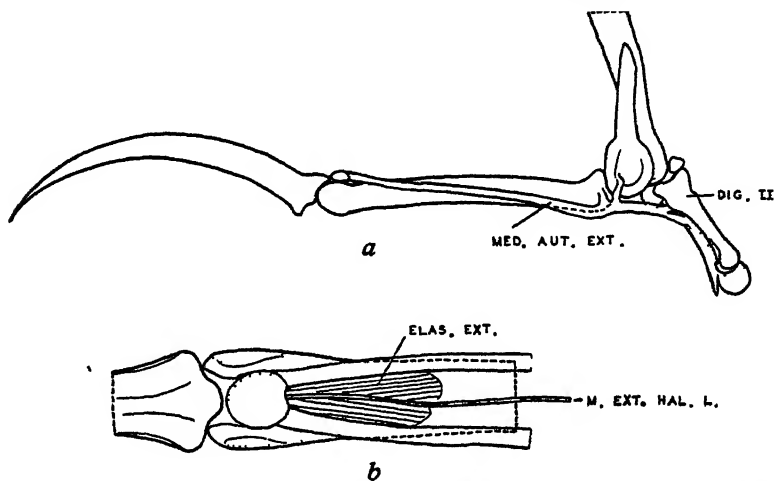
Fig. 15. Automatic extensor ligaments of claw of hallux as illustrated by *Certhia familiaris*. *a*, medial view of hallux and basal region of foot (× 5.1) showing medial automatic extensor ligament and its basal attachments on digits I, II, and III, and metatarsal I. *b*, Dorsal view of hallux at articulation of ungual phalanx (× 14.5) showing especially the sesamoid bone which serves in the common insertion of the extensor ligaments, the elastic extensor bands, and the M. extensor hallucis longus.

extensor digitorum longus and the concomitant relaxation of the toe flexors. Extension of the bases of the foretoes causes a strong and nearly direct pull on the automatic extensor ligaments and thus elevates the claw of the hallux. As a corollary, strong flexion of the claw of the hallux would cause the automatic extensors to flex the bases of the foretoes and thus strengthen the grasp.

This extensor device is well developed in *Sitta* and *Certhia*, where the large size of the hallux and its claw and the great arc of the claw suggest the importance of this digit in grasp and support while climbing. This must be true in *Sitta* especially, since its feet alone give support. The same device is present but less developed in *Thryomanes*, where apparently less need exists for such strong control of the claw. No such extensor device was found in *Dryobates*, where it would hardly be of use since the hallux is much reduced and functionally unimportant. In *Dendrocolaptes*, where the hallux is moderately reduced and the claw has a smaller arc, probably correlated with very efficient tail support, only the lateral part of this extensor device is present.

Tendinous pads and sesamoid bones.—Sesamoid bones are numerous in the birds dissected. There are long sesamoids in various tendons that course along the posterior side of the tarsometatarsus. The base of digit II of passerines

articulates almost entirely with two bones that apparently are sesamoid (fig. 16). Small sesamoids are often enclosed in the tendons of the ungual flexor and extensor muscles just before their insertion (fig. 15). The adaptive significance, if any, of these several bones is hard to determine. This is especially true since stiffening of tendons sometimes simulates the rigidity afforded by actual bone. Among the passerines, nevertheless, trunk climbing is correlated with possession of hard tendinous pads or sesamoids at ungual insertions. *Certhia, Sitta,* and *Dendrocolaptes* all have sesamoids at the insertion of the hallucal extensor muscle and the automatic extensor ligaments. Either markedly thickened tendons, tendinous pads, or sesamoid bones are usually at other ungual insertions. *Thryomanes,* however, has only one pad and no sesamoids. This difference is probably explained by the more exacting use of the claws and the necessity for their rigidity in trunk-climbing birds. Pads or sesamoids probably provide this advantageous rigidity to the claw by maintaining a direct pull of the tendons. *Dryobates* lacks such ungual sesamoids. Slight differences in the ungual articulations possibly compensate for this lack.

ACTIONS OF MUSCLES OF THE TAIL AND JAWS

Depressors of the tail.—The tail muscles of the species studied are qualitatively uniform, but show pronounced quantitative differences correlated with variation in the size of caudal vertebrae and pygostyles. Figure 13*g* represents such quantitative differences in the combined weights (of one side only) of all the muscles which depress the tail. These muscles comprise the caudofemoralis, depressor coccygis, pubicoccygeus externus, and pubicoccygeus internus. The low value for *Sitta* strikingly reflects the unimportance of its tail. In comparison, *Thryomanes,* which habitually uses the tail in balance or in flight, has a value more than 50 per cent greater. The closeness of *Thryomanes* to *Certhia* probably indicates that no especially great force is necessary to hold the tail against the tree in *Certhia.* However, the value for the depressors of the tail is 26 per cent greater in *Dryobates* than in *Certhia.* This may well be correlated with the more perfect modification of the tail feathers of *Dryobates,* and the greater emphasis on the feet for support in *Certhia.* Also, the drilling habits of *Dryobates* must demand more forceful support from the tail than do the probing habits of the creeper.

Muscles of the jaws and palate.—Engels (1940), working with thrashers of the genus *Toxostoma,* has demonstrated the correlation of increased arc of the bill with increased angle of insertion of the superficial part of the external mandibular adductor muscle. A greater angle is accompanied by an increasingly dorsal position of the origin of this muscle in the temporal fossa. The action of the muscle to pull back the lower jaw is greatest when the angle of insertion is small. This is disadvantageous in curve-billed forms because the grasping surfaces of the tip of the bill are thus pulled apart. The correlation between bill curvature and increased angle of muscle insertion was not found in the present study. For one thing, the arc of the bill even of *Certhia* is not as great as in most of the thrashers.

Judging from the posterior extent of the origin of the superficial part of

the external mandibular adductor, this muscle seems best developed in birds that use the bill forcefully. It is least developed in *Certhia* and *Thryomanes*, more developed in *Sitta* and *Dryobates*, and most developed in the wood-hewers. In woodhewers the muscle has a bipennate structure and extends far back on the surface of the skull. The apparently greater power of this muscle in birds that use the bill forcefully, whether for prying or pounding, may well be most significant as an indication of greater strength in closing the bill or in holding it rigid for pounding.

Engels also shows a positive correlation of the development of the retractor palatine portion of the M. pterygoideus with the thrasher's ability to dig by driving the bill into the ground and then pulling it rigidly backward. This retractor palatine muscle mass was decidedly better developed in *Sitta* than in either *Certhia* or *Thryomanes*. This greater development in *Sitta* seems to be associated with the need for rigidity when the bill is used in pounding, rather than with a need actively to depress the upper mandible.

EPIDERMAL FEATURES

Burt (1930) gives little attention to the adaptations of epidermal parts of woodpeckers. Eckstorm (1901), however, clearly analyzes many variations in such structures. Rictal bristles and the epidermal structure of the tongue are not dealt with here, although these features appear to be adaptive for trunk foraging in some species. Eckstorm (1901, p. 74) discusses the probable role of the rictal bristles of woodpeckers in protecting the nostrils. She also points out the puzzling similarity in the development of these bristles in some other birds, such as crows. Gardner (1925), especially, has made an extensive comparative study of the superficial structure of bird tongues. He describes, for instance, the piercing barbs on the tongues of woodpeckers, and figures or discusses the tongues of all the birds in the present study.

MODIFICATIONS OF TAIL FEATHERS

The correlation of stiffening of the tail feathers with the use of the tail for support in climbing is obvious. An analysis of the exact method of stiffening in different species, however, has revealed significant details and shown how different modifications toward the same functional end may enter into parallel adaptation.

Shaft or rachis.—The shaft of a supporting rectrix is strengthened, since it must effectively support the body. This is true whether its barbs or the tip of the shaft itself come into contact with the tree trunk. Figure 16 shows the magnified tips of the medial rectrices of both trunk-climbing and other birds. The distal parts of the shafts are better developed in trunk-climbing birds, exclusive of *Sitta*. The shaft is best developed in *Dendrocolaptes*, where it actually comes in contact with the tree trunk and must directly support a large part of the body weight. The shaft is similar in many swifts (fig. 16*f*), correlated with their roosting on vertical surfaces. The distal part of the shaft in *Dryobates* is tapered and flexible. As Eckstorm (1901, p. 97) points out, this flexibility probably allows all the large distal area of stiffened barbs to be

TABLE 6
Cross Sections of Bases of Rectrices in Per Cent of Trunk Lengths
(3 Specimens of Each)

Species	Rectrix I	II	III	IV	V	VI
Certhia familiaris..........	6.3 (6.2–6.4)	5.4	5.2 (5.1–5.4)	4.8 (4.3–5.1)	4.1 (3.6–4.3)	3.7 (3.6–4.0)
Dendrocolaptes certhia........	6.2 (5.9–6.3)	5.4	5.0 (4.9–5.2)	4.5 (4.4–4.6)	4.3 (4.1–4.4)	4.1 (4.1–4.2)
Dryobates pubescens	6.5 (6.4–6.6)	5.9 (5.7–6.2)	4.7 (4.4–4.9)	4.2 (4.0–4.4)	3.8 (3.5–4.0)	Vestigial
Sitta carolinensis.........	3.7 (3.5–3.8)	3.8	4.0 (3.8–4.1)	3.8	3.1	4.5 (4.4–4.6)
Thryomanes bewickii........	4.0 (3.9–4.2)	4.0 (3.9–4.2)	4.0 (3.9–4.2)	4.0 (3.9–4.1)	4.0 (3.9–4.1)	3.9

préssed against the bark, even when the proximal section of the shaft is at an angle to the bark (fig. 2).

Burt (1929, fig. 5, p. 437) compares cross sections of the bases of rectrices in woodpeckers. He shows that the relative size of the cross section of medial rectrices becomes greater with the increase in the habit of trunk climbing. This same correlation occurs in unrelated trunk-climbing birds (table 6), and is emphasized by comparison with birds that do not use the tail for support. Burt's use of a standard rectrix length as a basis of comparison seems inadvisable, since relative rectrix lengths vary.

The hypertrophy of the medial rectrices of species that employ the tail for support is correlated with the predominant part which these feathers play
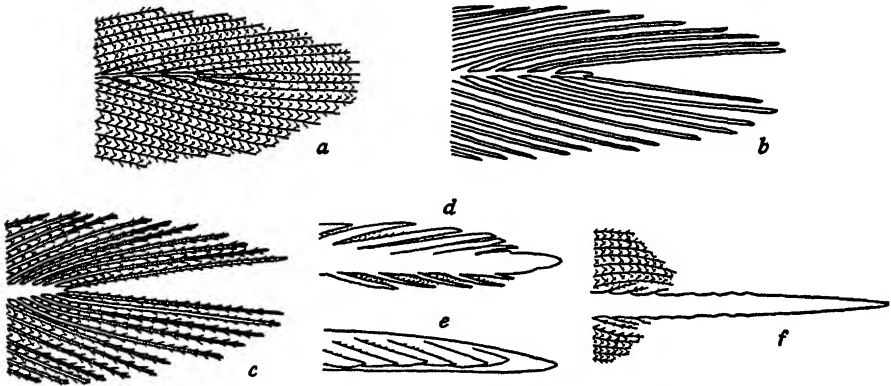
Fig. 16. Enlarged tips of medial rectrices. *a. Thryomanes bewickii*, × 10.7; *b, Certhia familiaris*, × 10.4; *c, Dryobates pubescens*, × 5.2; *d* and *e, Dendrocolaptes certhia*, × 7.9; *f, Chaetura vauxi*, × 7.9. With the exception of *Thryomanes*, which serves for comparison, all the figures are of rectrices which are used for support. Enlargements are of dorsal views except *e*, which is a lateral view. Barbules are diagrammatic: functional ones (interlocking) are represented by small lines whose tips cross; nonfunctional ones (because of separation, reduction, or loss of parts), by lines which do not meet.

and their stronger and closer binding to the pygostyle. The values for the more lateral rectrices are progressively smaller. This is correlated with their lesser importance for support. The most lateral rectrices (V and VI) are rarely used for support. The small values of the cross sections of medial rectrices in *Sitta* are probably correlated with the reduced lengths of these rectrices and the reduction of the use of the tail.

Rami.—Figure 16 also illustrates modifications of distal rami. A lateral thickening of the rami with a concomitant increased stiffness is a modification common to birds that use the tail for support. The thickening of these distal rami is also dorsoventral, their ventral ridges being greatly enlarged. This is definite in *Dryobates* and *Certhia*, but striking in *Dendrocolaptes*, where the rami become thick and platelike (fig. 16e). The distal rami are markedly lengthened in *Certhia* and *Dryobates*, as compared with *Thryomanes*. In *Dendrocolaptes* the rami play a secondary part in the transmission of support, and accordingly are short. This shortness does not seem to be associated with disuse, but rather with the freeing of the tip of the shaft so that it may come

TABLE 7
EXTENT OF AREA OF STIFFENED RAMI IN PER CENT OF TRUNK LENGTH
(3 Specimens of Each)

LATERAL EDGE

Species	Rectrix I	II	III	IV	V	VI
Certhia familiaris............	94 (80–101)	92 (85–99)	97 (87–109)	119 (109–130)	116 (98–138)	114 (109–116)
Dendrocolaptes certhia........	47 (44–49)	36 (33–42)	34 (27–37)	34 (25–41)	34 (26–38)	25 (22–32)
Dryobates pubescens..........	43 (37–51)	35 (33–40)	29 (18–37)	13	No stiffening	Vestigial

MEDIAL EDGE

Species	Rectrix I	II	III	IV	V	VI
Certhia familiaris............	72 (53–87)	27 (25–30)	25 (18–36)	19 (7–33)	16 (6–29)	11 (4–22)
Dendrocolaptes certhia........	33 (24–41)	20 (17–24)	15 (11–22)	13 (9–17)	13 (8–15)	8 (4–11)
Dryobates pubescens..........	43 (33–49)	39 (33–44)	31 (18–44)	17 (13–22)	No stiffening	Vestigial

into contact with the bark. In *Chaetura,* on the other hand, the most distal barbs are lost. Supporting rami are apparently not necessary in this bird, since the shafts of the rectrices alone seem sufficient for stationary vertical roosting.

No exact measurement of the length of the area of stiffened rami was possible, since these grade into the less stiffened rami. The area of stiffening was closely approximated, nevertheless, by microscopic examination and palpation. Measurements were taken on both the lateral and medial edges of a supporting rectrix, from its tip to the proximal limit of stiffened rami. Table 7 shows the approximate extent of modification of the rami in the rectrices of each species.

The high values for *Certhia,* especially for the lateral edges of rectrices, may be correlated with the great reduction, through wear, of the tail of this species. The low values for *Dendrocolaptes,* lower, on the average, than *Dryobates,* are probably explained by the strong use of the shafts for direct support. The low values for *Dryobates,* especially as compared to *Certhia,* probably indicate a shorter, more durable, and more efficient supporting tail. The table also indicates a greater use of the lateral than medial edges of rectrices for support in *Certhia* and *Dendrocolaptes.* The nearly equal use of the supporting edges in *Dryobates* is probably a more specialized condition accompanied by a special method of pressing the tail against the trunk. A further point shown in table 7 is the greater extent of the area of stiffened rami in the first rectrices as compared to the lateral rectrices. This corroborates other evidence showing these medial rectrices to be the most important in support.

Barbules.—The complete loss of the barbules of distal rami is one of the most marked modifications of the rectrices of *Certhia* (fig. 16 b). Barbules appear not far proximally from the tips of the rectrices, but the most distal ones are scattered and functionless. Such a loss of functional barbules seems to be correlated with the hypertrophy and heavy use of the individual rami. The distal barbules of *Dendrocolaptes* are reduced, scattered, and functionless (fig. 16 d). Also in *Dryobates* the barbules of distal rectrix barbs are not functional in interlocking; however, they are not reduced in number but are thickened and set at a smaller angle to the ramus, so that those most distal on a given ramus probably serve for support (fig. 16 c).

Lengths of rectrices.—Stolpe (1932, p. 212) has pointed out how increased tail length in a woodpecker would lessen the action of gravity tending to pull the bird outward from a vertical trunk. The weight of the body would be brought more directly over the distal, supporting end of the tail. This is theoretically true but cannot be applied unless various other factors can be controlled or understood. It is not safe to assume, for instance, that the angle of the shafts of the rectrices to the axis of the bird's body remains constant, or that the same length of the tail is pressed against the tree trunk in different species. The supporting rectrices of *Certhia* are not decurved as are those of *Dendrocolaptes* and *Dryobates* and, other things being equal, must be relatively longer in order to come into contact with the tree (see table 8). Also, the longer legs of *Certhia* (table 1) may well require a greater tail length if

TABLE 8

Lengths of Plucked Rectrices in Per Cent of Trunk Lengths

Species[a]	Rectrix I	II	III	IV	V	VI	VI/I	IV/I
Certhia familiaris	440 (416–464)	409 (394–423)	414 (380–440)	400 (360–427)	383 (348–410)	351 (330–376)	80	91
Dendrocolaptes certhia	344 (342–346)	322 (321–324)	306 (305–308)	290 (283–297)	271 (267–275)	248 (243–253)	72	84
Dryobates pubescens	284 (282–285)	271 (265–274)	257 (250–261)	245 (235–252)	226 (222–231)	Vestigial	80 V/I	86
Colaptes cafer	321 (304–320)	303 (295–306)	292 (286–296)	278 (271–284)	256 (250–259)	Vestigial	82 V/I	89
Thryomanes bewickii	336 (330–340)	342 (335–347)	337 (333–341)	325 (324–326)	312 (309–315)	281 (277–287)	84	97
Sitta carolinensis	258 (253–264)	269 (266–271)	269 (261–278)	270 (256–278)	269 (256–278)	269 (264–272)	104	105

[a] Three specimens of each; in each specimen the two rectrices of each pair are averaged.

the effectiveness of this supporting organ is to be maintained. Furthermore, in *Certhia*, the effect of shortening of the tail by wear would be offset if the tail were long at the start.

The shortness of the rectrices of *Dryobates* may be explained by its pecking and drilling habits, in which the head, and the trunk to some extent, often are drawn well back from the tree. In this position a short tail, by pushing outward on the postacetabular part of the body, acts both as a prop to keep the head in position for its often powerful, repeated blows and as a spring to help drive the head against the tree trunk. The hip joint is the hinge of this lever system. Such action would be less effective in a trunk climber with a long supporting tail, because the ventral angle of the rectrices to the median axis of the body would be larger. Also, the resiliency of the long tail, the tail being more nearly parallel to the tree, would push the bird upward rather than push the posterior part of the body outward. This hypothesis seems to be substantiated by the long tail of *Colaptes*, as compared to *Dryobates*, because this woodpecker does little drilling. The short tail of *Sitta* apparently is correlated with disuse or, in any event, the lesser importance of this organ.

Contact of tail with tree.—The lengths of the rectrices reflect the contact of the tail with the tree. The first pair of rectrices is always the longest in birds that use the tail for support (table 8). It is the most dorsal pair and so must extend beyond all the others if its tips are to be in contact with the tree. The medial rectrices are not the longest pair in *Thryomanes* and are the shortest pair in *Sitta*.

Eckstorm (1901, p. 90) points out in woodpeckers an apparent correlation between sharpness of tail, based on the ratio of the length of the outermost to that of the medial rectrix, and the amount of trunk climbing. This correlation is verified in the present study, for the ratio is smallest in all the species that use the tail for support. The ratios of rectrices IV/I are most indicative of this principle, since rectrix IV is actually used for support, whereas rectrix VI is not. Eckstorm (1901, p. 93) clearly shows how the rounded or pointed tail is best able to come into contact with the varying planes of the tree trunk. She also postulates (p. 98) that the different angles which the several supporting rectrices make with the tree trunk give an advantageous propping effect, especially in the sharper-tailed forms, because in these the angles made by the longest and shortest rectrices differ to a greater degree. This hypothesis is questionable or, at least, difficult to prove. Nevertheless, the assumption that a rounded or pointed tail is advantageous seems valid when one considers that the supporting barbs must come into contact with the bark.

The ventral curvature of the ends of shafts of supporting rectrices is apparently a modification to enable the tips of these rectrices to reach the tree without a disadvantageous increase in length. This is especially true of the first rectrices, and to a lesser extent of the second and third. Such a curvature is well marked in *Dryobates* and *Dendrocolaptes*. It is striking in the woodhewer *Pygarrhichas* (sometimes classified with the Furnariidae), in which all the rectrices arch sharply downward and thus bring the strong, pointed tips of their shafts against the tree trunk.

In *Dryobates* efficient contact of the ends of the first rectrices is made possible by the ventrally directed supporting rami, as well as by a curving of the shafts. Consequently, in ventral view, the supporting tips of these feathers are concave, in the form of a shallow V-shaped trough. The symmetry of this trough enables the slightly shorter and narrower distal ends of the second rectrices to lie in the trough and still have their supporting barbs exposed to the tree. The third rectrices fit similarly in the ventral troughs of the second, although at times, as when the bird alights, the tail is widely spread. Thus, the curving of the shafts, the ventral pointing of the rami, the symmetrical modification of rami for support on each side of the shaft, the graded lengths of supporting rectrices, and also the breadth of the supporting rectrix tips, combine to make the tail of *Dryobates* an efficient yet compact organ for support.

Certhia and *Dendrocolaptes* exhibit a condition which is partly comparable to the ventral direction of the supporting rami of *Dryobates*. The lateral supporting rami of their rectrices are directed ventrally, whereas the medial rami are horizontal or directed somewhat dorsally. Correlated with this (see table 7), the extent and strength of stiffened rami is much greater on the lateral than on the medial edges of rectrices. The resulting inefficient contact with the tree and the limited modification of medial rami probably necessitate a lengthening of supporting rectrices in order that the lateral rami may make sufficient contact to give the required support. Support is probably less efficient in *Certhia*, where the distal parts of the shafts do not firmly hold the rami or give direct support, as they do in *Dendrocolaptes*, until the rectrices are extensively worn.

Wear in rectrices.—The abrasion of supporting rectrices becomes increasingly noticeable until molting time. The extent of this wear ought to be a good criterion of the durability, and in a sense the efficiency, of the tail as a supporting organ. This would be especially true if the time and effect of molts, the effect of age of birds, and the effect of variations in trees habitually used, could be well understood. Measuring the wear of a tail is difficult, since this wear is likely to affect the different barbs, shafts, and rectrices in varying degrees. Nevertheless, a measure was selected which was sufficiently accurate and indicative to justify certain conclusions. The effect of molt and age can be judged well enough, and that of variable roughness of tree trunks disregarded, in a gross comparison.

The measure used was the length of the shaft of the first rectrix. The proximal point of reference was the binding between the first rectrices just posterior to the crest of the pygostyle. This measurement was especially practical since it could be taken on study skins as well as on preserved specimens. Representative specimens collected from September through November, after the annual molt, were used to obtain the normal unworn length of the rectrices. Specimens obtained in June or July, excluding the young of that year, were used in estimating the most worn condition of the rectrices. Such birds had used the same rectrices since the previous fall. Only *Certhia* (*C. f. occidentalis*) and *Dryobates* (*D. p. turati*) were compared. *Dendrocolaptes* is not compar-

able (see fig. 16) because the shafts, even of its unworn rectrices, normally serve for direct support.

The results of this comparison can be briefly summarized. The average unworn length of the shaft of the first rectrix of ten specimens of *Dryobates* was 53 mm. Of 12 specimens taken in June or July, 4 showed a slight reduction of these shafts, whereas the other 8 showed none. The distal barbs were somewhat shortened or broken in all summer specimens, but barbs modified for support were present even in the most worn tails. The greatest reduction of shafts of the medial rectrices in any of over 200 specimens was 9.5 per cent of the average unworn length of the shaft. In *Certhia* the average unworn length (in 15 specimens) of medial shafts was 59 mm. Of 26 adults taken in June or July, 9 showed a 40 per cent reduction of these shafts to the average length of 35.5 mm., whereas the other 17 showed a 13.5 per cent reduction to the average length of 51 mm. The extreme of wear (in over 150 specimens) was 61 per cent of the length of the unworn shaft. Typically, in the much worn group no modified supporting barbs were present, and the exposed shafts of rectrices, sharpened from wear, were alone responsible for support by the tail. In the less worn group, modified barbs still could play an important part in support, but were reinforced in this function by the exposed tips of the shafts.

The groupings into which the worn specimens of both *Dryobates* and *Certhia* seem to fall possibly reflect differences in age. Probably the tails of first-year birds are more easily abraded than those of older birds. The comparison illustrates that much greater wear commonly occurs in the supporting rectrices of *Certhia*, and substantiates the conclusion, drawn from various structural features, that the rectrices of *Dryobates* are more perfectly modified to give support.

ARCS OF CLAWS

The claws of trunk-climbing birds are visibly more curved than those of other birds. This might be expected because of the necessity of clinging to a vertical surface. Dependence on the claws, except for support from the tail, often becomes complete. Frequently only the tips of the claws hold the bird to the trunk, with no other parts of the digits touching (see fig. 2). The method used to measure the arcs of claws was essentially that used by Engels (1940, p. 352) for the arc of the upper mandible of curve-billed thrashers. The magnified claws were first drawn by the use of a camera lucida. Perpendiculars were then drawn to the halves of the bisected arc of the ventral outline of the claw in order to find the center of the circle of which this arc was a part. The central angle formed by radii drawn to the ends of a claw represents the amount of the circle of which the claw is a part. This measure is appropriate here, because the clinging power of a claw is determined by the fraction of a circle, in degrees, represented by the claw. Only the claws of digits I and III were measured (table 9), since digit III satisfactorily represents the grasping or clinging foretoes, whereas digit I shows its own distinct tendencies to atrophy or hypertrophy (tables 2 and 3).

Although these measurements show marked individual variation, such as is caused by wear and warping, certain general conclusions can safely be drawn

from them. The claw of digit I averages the least curved in *Dendrocolaptes*, in which species this digit is shortened probably concomitantly with the development of highly efficient tail support. This digit is extremely reduced in *Dryobates* but the arc of the claw remains great. Probably the claw of the hallux of *Dendrocolaptes* serves for support by pressing against the tree rather than clinging to it, whereas in *Dryobates* the hallux and its claw approach a vestigial condition apparently correlated with disuse and the lack of a demand for change. The great arc of the claw of the hallux and the hypertrophy of this digit in *Sitta* (tables 2 and 3) apparently reflect the need for

TABLE 9

ARCS OF CLAWS

Species	Number of specimens	Claw of digit I	Claw of digit III
Certhia familiaris	9	101° (85°–111°)	125° (105°–139°)
Sitta carolinensis	10	109° (96°–124°) (9 specimens)	105° (96°–125°)
Thryomanes bewickii	7	93° (76°–102°)	85° (78°–96°)
Dryobates pubescens	5	105° (89°–122°)	115° (103°–123°)
Dendrocolaptes certhia	3	90° (85°–94°)	148° (147°–148°) (2 specimens)

a strong grasping ability in this toe. This must be especially necessary in *Sitta*, since its tail is not used for support and its headfirst, downward climbing demands ability on the part of the hallux to cling fast.

Analysis of the claw of digit III can be made more readily than of digit I, because the claw of the third toe has a clinging function common to all trunk-climbing birds. The average arc of this claw is much smaller in *Thryomanes* than in the trunk-climbing birds studied. The lack of any overlapping of the extreme values validates the functional significance of this difference in arc. The great arc in *Dendrocolaptes* may be considered to be indicative of the highest development of clinging ability; it is perhaps correlated with the apparent lack of such ability in the hallux.

SIZE AND SHAPE OF HORNY BILL

Length of bill.—The significance of the length of the upper mandible has already been considered (fig. 10). The interpretation of this length was tentative, primarily because the length added to the bill by the rhamphotheca was not taken into account. *Total* lengths, measured from the tip of the bill to the

anterior tip of the lacrimal, are given in table 10. The interpretations based on the length of the upper mandible are verified by the total lengths. The comparison of these lengths shows the extent to which the rhamphotheca adds to the length of the bill. The rhamphotheca of *Sitta* and *Dryobates,* as compared to other species, has a greater extension anterior to the tip of the upper mandible. This greater development of horn seems to be correlated with pecking or drilling habits and a javelin-shaped bill. Probably the horn development reflects the wearing down of the bill by pecking or drilling. That horn is replaced rapidly is shown in woodpeckers prevented from using the bill in this manner. In these, the rhamphotheca may grow to such abnormal lengths as to preclude feeding.

TABLE 10

LENGTHS OF BILL AND UPPER MANDIBLE IN PER CENT OF POSTERIOR SKULL LENGTH

Species	Number of specimens	Upper mandible	Number of specimens	Bill	Per cent of total length added by horn
Certhia familiaris	11	98	9	119	21
Sitta carolinensis	15	86	6	116	30
Thryomanes bewickii	15	81	5	96	15
Dryobates pubescens	9	61	5	97	36
Dendrocolaptes certhia	1	143	2	154	11

Shape of bill tip.—Eckstorm (1901, pp. 68–74) analyzes the shape of the tip of the woodpecker's bill on a functional basis, and points out significant differences between species of woodpeckers. The vertically wedge-shaped bill tip of drilling woodpeckers was found only in the woodhewer *Pygarrhichas,* among other groups, and there it was not highly developed. This reflects the probability that no other birds have the drilling ability possessed by woodpeckers. The tip of the bill of *Sitta,* although acuminate, is evenly rounded and not suited for drilling. The tip of the bill of *Glyphorhynchus* is rounded and flattened from side to side, and although suited for transmitting forceful blows, would not be an effective drill. The tips of the bills of *Certhia, Thryomanes,* and *Dendrocolaptes* are decurved, the last being moderately hooked. Such curvature precludes a forceful direct pecking action but not a powerful digging action. Curvature may actually improve the digging, as Engels (1940, p. 356) points out in thrashers, by causing a greater displacement of material, such as dirt or rotten wood, when the inserted bill is drawn outward and backward.

SUMMARY AND DISCUSSION

It was expected at the outset of this work that trunk-foraging birds could be shown to have in common a number of adaptive modifications which would be lacking in other birds. This expectation has been realized only in part, such adaptations being restricted to the legs and feet. Examples are the shifting of the insertions of the iliofibularis and the tibialis anterior muscles, and the large size of the tibialis anterior. Actually, trunk-foraging birds are not closely

comparable to each other unless their methods of feeding and climbing are similar in detail.

Trunk-foraging birds that use the tail for support in climbing show many more structural adaptations in common than do trunk-foraging birds as a whole. Thus, a close comparison is possible between *Certhia, Dendrocolaptes, Glyphorhynchus,* and *Dryobates* because all use the tail for support. Examples of adaptations consistently correlated with this habit are strengthening of the shafts and rami of the supporting rectrices, and increased size of the pygostle and caudal vertebrae. A still closer comparison can be made between *Certhia* and *Dendrocolaptes,* in which the use of the bill is similar, and in like fashion between *Glyphorhynchus* and *Dryobates.* Members of these pairs of genera have additional adaptations in common, such as the shape of the bill or the strengthening of the skull for support.

Sitta differs from the other trunk-foraging birds because it does not use the tail in climbing. This, combined with the relatively infrequent use of the tail in flight and balance, has apparently led to a reduction of the rectrices and of the skeletal parts of the tail. With respect to use of the bill, *Sitta* is most like *Glyphorhynchus* and less like *Dryobates.*

Parallel adaptation for trunk foraging is least between *Certhia* (or *Dendrocolaptes*) and *Sitta.* It is greatest between *Certhia* and *Dendrocolaptes.* However, even if we choose the clearest possible case of a parallel adaptation, such as the strengthening of the rectrices for support in climbing, the structural convergence is still not complete. The shafts and barbs of the supporting rectrices of *Certhia, Dendrocolaptes,* and *Dryobates* are all strengthened, but they are modified in distinctly different fashions. Such differences may often be explained by the fact that comparable trunk-climbing birds have their adaptations variously emphasized even though their habits seem nearly identical. *Certhia,* for example, possesses less efficient tail support than does *Dendrocolaptes,* but probably has a more powerful grasping foot. Less evident compensatory adaptations, as in the size or action of muscles, undoubtedly exist but are usually not readily found or evaluated.

A question raised by this study is whether or not species differ in the perfection of their adaptation for trunk foraging. Perfection is difficult to judge, especially when unrelated birds are compared, and when compensatory adaptations exist. Nevertheless, comparison of *Certhia* with *Dryobates* indicates a less perfect adaptation for trunk foraging in *Certhia.* Rectrices, muscles, and skeleton of the tail are more modified in *Dryobates* than in *Certhia.* The tail of *Certhia* is typically much more abraded by use. The legs and feet of *Certhia* are also generally less specialized than those of *Dryobates.* Comparison of *Certhia* with *Dendrocolaptes* again indicates that *Certhia* is less specialized. The probable phylogeny of these birds may explain such differences. The relative perfection of the adaptation of woodpeckers and woodhewers, and the diversification within these groups, suggest that these birds represent old families. The creepers, judging from their close relation to advanced types of passerines such as wrens, and from their lack of diversification, are comparatively recent.

Robson and Richards (1936, pp. 348–353) emphasize the confusion with respect to the meaning of "adaptation." I use it in the same sense as have Engels and Miller, considering adaptations to be structural modifications mechanically suited to the use to which they are put. Classification of such adaptations is of value inasmuch as it usually indicates an understanding of the conditions which have led to them. Engels (1940, p. 396) divides the adaptations found in thrashers into three categories: primary adaptations, or modifications which seem directly correlated with particular habits; preadaptations, modifications which exist in ancestral species but seem to be of particular adaptive value only in more specialized, related species; and incidental adaptations, or those occurring with, but only secondarily related to, the habits correlated with the primary adaptations. Classification of the adaptations discussed in this study is not always possible, since this is not a study of a series of related forms. Consequently, tracing the history of adaptations is often precluded.

Types of primary adaptation are best exemplified by trunk-foraging birds. The chief types may be grouped as follows:

(1) Expansion of bone for stronger or more extensive attachment of muscles or connective tissues. Examples: Large size of the disc and crest of the pygostyle or of the transverse processes of caudal vertebrae of species that use the tail for support.

(2) Expansion of bone to withstand shock. Examples: Breadth of base of the bill or completeness of the interorbital septum of species that use the bill in pounding.

(3) Changes in length of bones for more efficient climbing and feeding. Examples: Great length of digit IV in all trunk foragers; shortness of the hind limb of woodhewers and the hallux of woodhewers and woodpeckers.

(4) Modification of the angle of articulation to permit advantageous positions of the distal parts. Examples: Articulations of the pygostyle or of the fourth toe of species that use the tail for support.

(5) Shifting of the tubercle of insertion of a muscle to increase the leverage of that muscle. Examples: Distal insertion of the M. iliofibularis and the tibialis anterior in trunk foragers.

(6) Increase or decrease in relative bulk of a muscle correlated with excessive use or disuse. Examples: Large size of the M. tibialis anterior in trunk climbers, and the gastrocnemius in other species.

(7) Possession of devices for more effective control of the claws in climbing. Example: Strongly developed automatic extensor ligaments of the claw of the hallux in trunk-climbing passerines.

(8) Changes in size or shape of the horny bill and claws for particular feeding habits or clinging ability. Example: Length and curvature of the fore claws in trunk climbers.

(9) Modification of rectrices for support of the body. Example: Thickening of shafts and rami of the supporting rectrices of species that use the tail in climbing.

Preadaptations (Engels) for trunk climbing are few, compared to primary

adaptations, and are less easily recognized in this type of study. The great length of the hallux in *Sitta* and *Certhia* seems to be a preadaptation, since the hallux also is long in *Thryomanes*. A long hallux probably is advantageous in *Thryomanes,* but especially, and in a somewhat different way, in *Sitta* and *Certhia* because of their dependence on this toe in trunk climbing. The short leg of *Dryobates* is of advantage in keeping the body close to the tree. It, too, is probably a preadaptation, since the legs are also relatively short in generalized Picoidea. The zygodactyl foot type which woodpeckers have in common with nonclimbing picoideans may well be a preadaptation. The long and variably reversible fourth toe must be especially valuable in making an efficient clinging foot for trunk climbing.

No well-defined examples of incidental adaptation were found. The value of this category is often doubtful, since modifications often seem to serve two equally important ends. For example, the bill of *Sitta,* because of its length and straightness, is adapted for both probing and pounding. Neither of these features can be considered incidental to the other.

In the flicker the characteristic picine structure of the bill and the tail appear more closely associated with infrequent activities, such as nest excavating, than with those connected with foraging. However, the correlation of these structures with foraging habits in other woodpeckers suggests that in *Colaptes* the structures were once primarily related to feeding. This does not deny the view of Burt (1930, p. 522) that the flicker, because of its lesser degree of specialization for trunk foraging, is a rather generalized woodpecker. It suggests that this species has descended from trunk-foraging forms, and has retained primarily trunk-foraging adaptations chiefly because of their continued occasional use, even if not in foraging. The long tongue of the flicker is apparently adapted for ant eating, whereas in other woodpeckers it is an adaptation for feeding on wood-boring insects. Therefore the long tongue of the flicker is probably a preadaptation.

I assume that adaptations are fundamentally hereditary, rather than that they are developed in the course of the lifetime of an individual. That this is a general truth is shown by the young of specialized animals. The young possess the adaptations of their parents, even though these adaptations have not yet been used. The tails and bills of nestling woodpeckers, for example, are essentially like those of the adults. Enough work has been done (Burt, 1930, p. 475, fig. 4; and Miller, 1937, p. 39, fig. 10), however, to show that adaptative structures can be modified late in ontogeny. The occurrence and extent of the influence of environment on basically hereditary adaptations should be thoroughly studied.

CONCLUSIONS

Adaptations are formed by the modification of previously existing structures. Structures can thus be modified so as to become almost unrecognizable, but often only a slight quantitative modification may be of adaptive significance. It seems a general rule that the structures modified were formerly adaptive in some way, and that the new adaptations typically result from changes in emphasis of the original functions. Thus, the nature of an adaptation is best

understood in comparison with the most closely related form which lacks this adaptation or adaptive emphasis. This principle is clear even in the present study of species that are not closely related, because homologous structures are compared. The principle does not apply in a comparison of phylogenetically distant forms in which nonhomologous structures can be adapted for the same function.

A strict classification of adaptations on the basis of associated habits is not possible because of great variation in adaptations and habits, as well as differences in plasticity of structures with regard to adaptive change. Nevertheless, adaptations appear most frequently and inseparably correlated with feeding activities. This might be expected from the fact that the greatest part of the activity of an animal is devoted to obtaining food. Almost all the adaptations considered here relate to feeding. The swift (*Chaetura*) is of special interest in that the modification of its tail for support is associated only with roosting and nest-building habits. Adaptations thus are not necessarily correlated with the most frequent instinctive actions, but can be correlated with more passive or less frequent vital actions. Also, an adaptation which is correlated with feeding habits may also be correlated with, and probably partly determined by, another habit, even though this habit is not practiced frequently. The bill of the nuthatch exemplifies this, since it is adapted for pounding as well as for digging, although digging is typically confined to a short part of the nesting season of each year.

I have not obtained conclusive evidence with respect to the manner in which adaptations are formed and persevere in phylogeny. Admittedly, the doctrine of use and disuse is convenient when one is trying to explain correlated adaptive changes in degrees of development of parts of a structure, as A. B. Howell (1930, p. 2) argues convincingly. A mutational explanation of adaptations is more acceptable because it explains the origin and the means of inheritance. However, to satisfy the conditions of many adaptations, mutations must be considered to be extremely numerous, they must be selected so as to make an effective adaptation, and they must be of such a nature that they may sometimes effect very small quantitative changes in interdependent characters.

Natural selection seems to be confirmed by the very existence of structural adaptations. The marked modifications needed for habitual trunk foraging, and the rather sharp separation of birds of such habits and structure from other birds, suggest that intermediate forms have been lost through the adverse action of natural selection. At the same time, the advantage accruing from trunk-foraging habits, assuming that population pressure has been effective in the past, is demonstrated in that numerous birds have come to subsist by such foraging habits.

This has been a study of parallel adaptation, rather than of convergence, because the structures compared are in every case homologous. The use of homology as a basis for the separation of these two categories of adaptation has been most clearly propounded by Abel (1912, pp. 624–625). This basis seems decidedly better than the view that convergence deals with unrelated animals and parallelism with related animals. Probably no rigid distinction

between parallel and convergent adaptation can be maintained, however, because of the complexity of types of adaptation and of the structures involved. The essentially nonhomologous adaptive structures in examples of convergence not infrequently are homologous to some degree.

The adaptations resulting from parallel or convergent evolution are often similar in their grosser aspects, but their details, however, are not effected by exactly the same modifications. Miller (1937, p. 64) has brought out this fact in genera of geese. It is well re-emphasized in trunk-foraging birds, because here even such specialized and similar structures as feathers are variously modified for almost precisely the same adaptive end.

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A NEW RACE OF WOOD RAT
(NEOTOMA LEPIDA)

BY

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(Contribution from the Museum of Vertebrate Zoölogy of the University of California)

In ORGANIZING an account of the mammals of Nevada, specimens of the desert wood rat, *Neotoma lepida,* from along the Colorado River in extreme southern Nevada were found to differ from any previously named kind. Study of these specimens and additional material from farther south in California reveals the existence of a previously unrecognized subspecies which may be named and described as follows:

Neotoma lepida grinnelli new subspecies

Desert Wood Rat

Type.—Male, adult, skull with skin; no. 10438, Mus. Vert. Zoöl.; Colorado River, 20 miles above (by river, but about 12½ miles north by air-line) Picacho, Imperial County, California; April 13, 1910; collected by Frank Stephens; original no. 2694.

Range.—Colorado River Valley from Boulder City, Nevada, south to Mexican Boundary and west in Colorado Desert to Beal Well.

Diagnosis.—Body short; tail long (80 to 95 per cent of length of head and body); color pale; tympanic bullae well inflated.

Measurements.—Average and extreme measurements in millimeters of 5 adult males and 4 adult females, from the type locality and along the Colorado River as far northward as 4 miles south of Palo Verde, are: Total length, ♂, 291(288–295), ♀, 298(286–310); length of tail, 134(118–145), 142(137–147); length of hind foot, 30.4(29–32), 30.3(29–32); length of ear from notch, 29.8(28–32), 29.7(29–31); weight of one of each sex, 154.7, 130.8 grams; basilar length, 32.6(30.6–34.2), 32.2(32.0–32.5); zygomatic breadth, 20.5(19.9–21.0), 20.4 (20.2–20.6); interorbital breadth, 5.1(4.9–5.3), 5.1(4.9–5.2); length of nasals, 14.7(14.0–15.8), 14.8(14.3–15.1); length of incisive foramina, 8.3(8.0–8.6), 8.3(8.1–8.4); length of palatal bridge, 6.9(6.6–7.1), 6.9(6.5–7.3); alveolar length of maxillary tooth row, 8.2 (8.0–8.4), 8.2(7.9–8.3).

Specimens examined.—Total number, 80, from the following localities: NEVADA, *Clark Co.:* 4½ mi. W Boulder City, 2600 ft., 1; Colorado River, 14 mi. E Searchlight, Jap Ranch, 500 ft., 4; 8 mi. S Dead Mtn., 2700 ft., 3; Hiko Spring, 8 mi. SSE Dead Mtn., 1900 ft., 5; Colorado River, ½ mi. N California–Nevada Monument, 500 ft., 5. CALIFORNIA: *San Bernardino Co.:* 3 mi. E Mt. Manchester, 12 mi. N Needles, 7; opposite The Needles, Colorado River, 3; 25 mi. S Needles, 475 ft., 2; 950 ft., Whipple Mts., 1; Horn Mine, E base Turtle Mts., 14 mi. NE Blythe Junction, 7. *Riverside Co.:* Riverside Mt., Colorado River, 2. *Imperial Co.:* 9 mi. NE Beal Well, 1996 ft., 1; 4 mi. S Palo Verde, 275 ft., 2; Beal Well, 1346 ft., Chocolate Mts., 2; opposite Cibola, Colorado River, 1; Arroyo Seco, 12 mi. S Palo Verde, 1; 20 mi. above Picacho, Colorado River, 12; 13 mi. NE Glamis, 4; 8 mi. below (east) Picacho, Colorado River, 3; 2 mi. NW Potholes, 250 ft., 1; Potholes, Colorado River, 2; Pilot Knob (and near Pilot Knob), Colorado River, 11.

Comparisons.—From *lepida* this race differs in actually and relatively longer tail, slightly lesser average size in most other parts measured, and lighter color. From *monstrabilis,* the race to the east along the north side of the Colorado River, *grinnelli* differs in longer tail and grayer (less buffy)

color. From *devia,* the race to the east in Arizona south of the Colorado River, *grinnelli* differs in longer tail, lighter color, and shorter interparietal. From *felipensis,* the race in northeastern Lower California, *grinnelli* differs in shorter hind foot and ear, slightly darker coloration on the average, and narrower rostrum. *N. l. felipensis* averages larger than *grinnelli* in most parts measured. From *gilva,* the race to the west, *grinnelli* differs in smaller size throughout, relatively shorter tail, color of upper parts with less blackish, and more inflated tympanic bullae on which the anterior lip of the meatus is more prominent.

Remarks.—By analogy with the geographic variation occuring in *Peromyscus crinitus* and some other members of the family which occur over the same region, a longer tail is to be expected in this race than in more northern populations of the species which are referred to the races *nevadensis* and *lepida.* In advance of study it was supposed that individuals of *felipensis,* the race in northeastern Lower California, had tails longer than individuals of the race *grinnelli.* Nevertheless, in the southern populations of *grinnelli* the tail is relatively longer, although actually of about the same length as in topotypes of *felipensis.*

In the Colorado Desert, Beal Well is the westernmost known station of occurrence of *grinnelli.* Specimens from farther to the north at Clemens Well, Shaver Summit, and Dos Palmos, all three places on the eastern side of Salton Sea in Riverside County, and animals in San Bernardino County from Twenty-nine Palms and the Sheep Hole Mountains, are referable to the race *lepida.* Specimens from Dos Palmos Springs in the Santa Rosa Mountains of Riverside County, and La Puerta in San Diego County, have been referred to the race *lepida* rather than *gilva,* but these specimens have small tympanic bullae like *gilva* and unlike *lepida.* They appear to be intergrades between *lepida* and *gilva* and have no close relation to *grinnelli.* The name *grinnelli* may be applicable to animals of the species *lepida* from the eastern side of the Colorado River in Arizona. Benson (Occas. Papers, Mus. Zoöl., Univ. Mich., no. 317, p. 6, July 1, 1935) points out that animals along the eastern side of the river near 34° N latitude have longer tails than do populations farther north and east, to which the name *devia* is appropriately applied. In its lower course, the river is not as effective a barrier as farther north, where shifting of rat-inhabited blocks of land from one side of the river to the other occurs less often, if ever. For the time being, until more adequate material from the eastern side of the river is available, the animals there may best be referred to *devia* although they are unlike topotypes of that race.

The name *grinnelli* is proposed in recognition of the important contributions made to our knowledge of the land vertebrates of the valley of the lower course of the Colorado River by the late Professor Joseph Grinnell, who in "An account of the mammals and birds of the lower Colorado Valley with especial reference to the distributional problems presented" (Univ. Calif. Publ. Zoöl., vol. 12, pp. 235–237, 1914) gives information on the habitat in which the animals here newly named were found.

THE NATURE OF THE RED, YELLOW, AND ORANGE PIGMENTS IN WOODPECKERS OF THE GENUS COLAPTES

BY

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BY

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(Contribution from the Museum of Vertebrate Zoölogy of the University of California)

THE BRIGHT and many-hued plumages of birds offer challenging problems to students of evolution, the solution of which has long been hindered by lack of information about the chemical nature of pigments. But the last few years have seen rapid progress in the difficult techniques used in determining the chemical structure and properties of pigments. Carotenoids form one of the two principal groups of pigments in the plumage of birds and are responsible for many of the yellows, oranges, and reds.

As one phase of a study of the evolution of coloration in flickers, genus *Colaptes,* I have deemed it advisable to identify the pigments involved. This genus of woodpeckers has held the special interest of biologists ever since it was found that two kinds (*Colaptes auratus* and *C. cafer*), of strikingly different coloration and each possessing an extensive breeding range of its own, apparently interbreed throughout a large area in the western United States and Canada. In this area most of the flickers exhibit, in many ways and degrees, combinations and/or intermediate conditions of the color characteristics of the two kinds. For example, the under side of the wings and tail, which is red in one of the species and yellow in the other, may be some hue of orange-red, orange, or orange-yellow in the "hybrid" individuals. Of the other three species of flickers, *C. chrysocaulosus* closely resembles *auratus* and inhabits certain West Indian islands; *C. chrysoides* and *C. mexicanoides* have more characteristics in common with *cafer; chrysoides* lives in the southwestern United States and northwestern Mexico; *mexicanoides,* in northern Central America.

The red, orange, and yellow pigments of the flickers occur most prominently in the feathers of the wings and tail of both sexes of all five species and in the malar stripes of the males. They occur in lower concentration in most of the feathers of the body, where they are partly or wholly masked by brown or black melanic pigments. Although similarly masked on the upper sides of the wing and tail, they are exposed on the under sides of the rami and shafts, imparting a bright yellow, orange, or red hue to the entire surface. In the malar feathers of the males of some kinds of flickers the red pigments are completely masked by melanins.

Preliminary tests with extraction showed that these bright pigments are not water-soluble but that they can be extracted with the fat solvents, methanol, ethanol, and carbon disulfide. According to Fox (1936:483), these facts provide evidence of the carotenoid nature of these animal pigments. Carotenoids are widely distributed among organisms, especially plants. They

are polyene hydrocarbons, alcohols, and ketones, whose colors are apparently produced by the long conjugated chain of double-bonded carbon atoms in each. Most animals, perhaps all, appear to be dependent on plants for their supplies of these pigments, for, although able to modify them after ingestion, animals have not been shown to have the ability to perform the basic synthesis. Among the best reviews of the chemical, physiological, and biological aspects of carotenoids, and of the techniques for their identification, are papers by Bogert (1938), Kuhn (1935), Lederer (1934, 1935), Miller (1935), Palmer (1922), Strain (1938), Zechmeister (1934), and Zechmeister and Cholnoky (1937).

ACKNOWLEDGMENTS

TECHNIQUE

The feathers to be extracted were carefully examined for similarity of color and for freedom from foreign materials; soiled parts were discarded or washed clean with water. Sometimes it was necessary to combine feathers from two or more birds to obtain enough pigment.

All feathers larger than malars were cut into small pieces with scissors, after the shafts were split. Extraction was carried out either in a bronze ball mill (Sumner and Fox, 1935: 333, 339) or by grinding with cleaned sand using mortar and pestle. The mortar-and-pestle method was found to be slow, difficult, and otherwise unsatisfactory. In both methods, enough pure methanol was used to cover the mass of feather parts. After 45 minutes in the mill, the supernatant solution of pigment was decanted, an equal volume of fresh methanol added to the feather mass, and the mill operated for another 30 minutes. By then the pigment usually was completely removed from all but the larger pieces of shaft. Using mortar and pestle the feathers were ground as thoroughly as was possible in 20 or 30 minutes, the supernatant solution decanted, and fresh methanol added to the feathers. They were then put in the dark in a refrigerator to soak for 24 hours, at the end of which time they were again ground for several minutes. This removed most of the pigment, but the larger pieces of feather were still somewhat colored. Solutions of pig-

ments not in use were always kept under an inert gas, either nitrogen or illuminating gas, in a refrigerator.

Grinding with sand did not result in rapid oxidation of the carotenoids, as it has been found to do with fresh leaves. Strain (1938:115–117) has suggested that enzymes probably are responsible, at least in part, for the rapid oxidation. Feathers, being completely dead when mature, presumably are without enzymes. The same author has suggested that the physicochemical state of the carotenoids in the plant cell, or the oxidation of associated labile substances, may also influence the oxidation of the carotenoids. Their state in feathers is not known, except that they appear to be diffused rather uniformly through the keratin.

After extraction was completed, the last solution and the previously decanted portion were poured onto a sintered glass filter and filtered with gentle suction. The extraction apparatus was rinsed with methanol and the rinsings were filtered. The extracted feather mass was then washed with successive portions of methanol until the washings were colorless.

The methanol solution of pigments was next transferred to a separatory funnel and to it was added one-ninth of its volume of distilled water and ten-ninths of petroleum ether. The mixture was agitated, and then the solutions were allowed to settle. Both layers always became at least slightly colored, indicating either that more than one group of carotenoids was present or that part of the pigment was esterified. The lower layer, of 90-per cent methanol, was then drawn off into another separatory funnel and to it was added an equal volume of petroleum ether; extraction was carried out as before. The lower layer was again drawn off and the petroleum ether solution was added to the main portion obtained in the first extraction. The combined portions were then extracted with an equal volume of 90-per cent methanol and the extract added to the other portion of methanol solution. Several successive extracts were thus made from the two solvents, the extract each time being added to the main portion of the same solvent, until the amount of pigment extracted was apparently at a minimum. It never was possible to make an absolute separation of pigments with this partition method; the extracting solvent was always at least slightly colored. These results agree with those of Strain (1938: 33–34), who found that even under the most favorable conditions this method did not always produce quantitative separation of carotenes and xanthophylls in a mixture of pigments extracted from leaves.

After this separation, the petroleum ether solution was washed with eight to ten successive portions of distilled water, at first merely by running the water through the solution from above, later by gentle mixing, and finally by vigorous shaking. The petroleum ether solution of epiphasic pigments was then dried in a flask with sodium chloride and placed under an inert gas in the dark in a refrigerator until it could be chromatographed.

The pigment in the 90-per cent methanol was forced into petroleum ether by adding successive portions of the ether and of distilled water to the methanol in a separatory funnel. The solvents were mixed each time by

inverting the funnel, then allowed to separate, and the lower layer of methanol was drawn off before the petroleum ether extract was poured into another funnel. A small volume of water was added for the first extraction, the amount being gradually increased in succeeding extractions. The extracted methanol was discarded.

The combined portions of pigment in petroleum ether thus obtained were thoroughly washed, then dried with sodium chloride. The dried solution was concentrated to a few milliliters in an Ehrlenmeyer flask in a warm water bath while a stream of illuminating gas or nitrogen played on the solution. In this process considerable amounts of colorless contaminants were deposited on the walls of the vessel.

To determine whether this hypophasic pigment was composed of only one kind, or, as seemed more probable, several, it was chromatographed on a Tswett column of calcium carbonate. This method for the separation and purification of carotenoids has been thoroughly discussed recently by several workers, especially Miller (1935), Strain (1938), and Zechmeister and Cholnoky (1937). In the light of the more recent papers, improvements could probably be made in the procedure described below.

A tube 2 cm. in diameter, with a sintered glass filter in the bottom, was packed to a depth of about 7 cm. with calcium carbonate that had been oven-dried for 5 hours at 150° C. and kept in a desiccator over calcium chloride until used. The finely powdered carbonate was packed dry, by use of a cork on the end of a stick. Enough powder was added at a time to form a 5–10 mm. segment when tightly packed. This method was found to give a column of good uniformity and was easier than wetting the carbonate with petroleum ether before packing. The adsorbed bands of pigment were even more uniform than when the column was made wet. After completion of the column, petroleum ether was poured gently onto it, a slow stream of illuminating gas or nitrogen run into the tube through a cork which partly closed the top, and suction applied. Petroleum ether was added until the column was completely wet.

Onto the wet column was poured the concentrated solution of carotenoid in petroleum ether while suction was continued, and an inert gas played on the solution. The pigment was adsorbed in a single band at the top of the column, but in extracts from flight feathers this band broke into two or more bands as the less easily adsorbed pigments washed down. The column was washed with petroleum ether until the bands stopped moving; they were only slightly separated and were near the top of the column.

At this stage the chromatograph was "developed" with benzene (C_6H_6), the addition of which sometimes appeared to rearrange the bands and always caused them to move down through the column, separating further as they did so. The most satisfactory combination of separation and definition was achieved by the addition of about 12 ml. of benzene. If the lowest band washed through into the filter flask, it was necessary to stop suction before the next band came through.

After development, the tube was removed from the flask and each band dug out as quickly as possible, the uppermost first. The carbonate bearing each band was put into a separate flask and covered with petroleum ether. In digging out two bands that were close together, a shallow intermediate layer that appeared to contain pigment of both bands was sometimes discarded. Bands were sometimes so close together that they were dug out as a unit and rechromatographed.

Sometimes petroleum ether alone was sufficient completely to elute the pigment from the carbonate, but usually the addition of a few drops of methanol was necessary. After elution, the solutions were filtered on a small sintered glass filter under illuminating gas with gentle suction and the clear filtrates each evaporated in a hot (not boiling) water bath under illuminating gas.

Each residue, which appeared to be at least partly crystalline, was taken up in carbon disulfide and stored under an inert gas in a refrigerator until spectrophotometric examination could be made. A small amount of colorless contaminants usually remained on the walls of the evaporating vessel.

Attention was then directed to the epiphasic fraction if it contained sufficient pigment. This solution was evaporated on the water bath, the oily orange-red residue taken up in about 50 ml. of 95-per cent ethanol, and the resulting solution transferred to a 125-ml. flask fitted with a ground-glass stopper. Ten per cent, by weight, of potassium hydroxide was added and the solution kept in a bath of hot water (below the boiling point of the solution) for three hours. The ground-glass stopper was set in loosely and allowed release of pressure when it became too great. The amount of evaporation was small.

After three hours of hydrolysis the pigment solution of alcoholic alkali was diluted with 95-per cent ethanol and placed in the separatory funnel (considerable amounts of colorless contaminants remained on the walls of the hydrolyzing vessel), and an approximately equal volume of petroleum ether was added, followed by a small amount of distilled water to cause separation. Most of the pigment usually migrated to the upper layer. The alcoholic alkali was drawn off and extracted with successive portions of petroleum ether and increasingly larger amounts of water. Three extractions were usually sufficient for complete transfer of the pigment.

The petroleum ether extracts were combined, washed thoroughly, and dried with sodium chloride. To the dry solution was then added an equal volume of 90-per cent methanol, and the partition of pigment noted after agitation in a separatory funnel. Most of the pigment remained in the petroleum ether. The alcoholic solution was not followed further.

The petroleum ether solution was washed, dried, concentrated to a few milliliters, and chromatographed as described previously for the hypophasic fraction. Each band was dug out, the pigment eluted, and the resulting solution filtered. The filtrates were evaporated and the residues taken up in carbon disulfide for spectrophotometric examination.

Absorption spectra have been used for a long time in the description and

identification of carotenoid pigments. Strain (1938:42–45) and Bogert (1938:1173) emphasize the value of the determination of absorption curves, which are characteristic of each pigment. Such a curve is obtained by plotting units of relative intensity against wave length. With the Bausch and Lomb instrument used for most of our work, the intensity ($d = \log I_0/I$, where I_0 is the intensity of the light passing through a given layer of solvent alone, and I the intensity of that through an equal layer of solution of pigment) is read directly from a revolving disc and is determined by visual matching of the light intensities.

ANALYSIS OF PIGMENTS

CAROTENOIDS OF THE FLIGHT FEATHERS OF C. AURATUS

All the flight feathers of a male *C. a. luteus* taken September 2, 1938, at West Lafayette, Tippecanoe County, Indiana, were extracted. The flight feathers in this species are clear lemon-yellow. Partition between petroleum ether and 90-per cent methanol showed both an epiphasic and a hypophasic fraction. Chromatographing of the hypophasic fraction showed two main bands about 12 mm. apart and yellow-orange in color. Below the lower one were some faint bands which did not contain enough pigment for analysis. The absorption curves (fig. 1) of the principal pigments in carbon disulfide, made with a photoelectric spectrophotometer, have maxima as follows: band *a* (upper band), 470 and 501 mμ; band *b* (lower band), 473 and 501 mμ. Comparison of these values with those given for known carotenoids by Strain (1938:18–30) shows that the pigments are xanthophylls (carotenols of Bogert, 1938:1140), perhaps closely related to eloxanthin (maxima, 472 and 502), taraxanthin (maxima, 469 and 501), and violaxanthin (maxima, 469 and 500.5).

A chromatograph of the unsaponified epiphasic fraction showed bands as follows (top to bottom); the column was washed only with petroleum ether:

a. Yellow band about 20 mm. from top of column. An orange and a yellow band about 55 mm. farther down; these removed together and rechromatographed, using benzene (C_6H_6) for developing. This treatment produced bands:

    b. bright orange with a trace of yellow;

    c. diffused pale orange band below *b.*

d. This pigment not adsorbed, but washed through into filter flask.

The absorption maxima, in mμ, of these pigments in carbon disulfide, taken with a photoelectric spectrophotometer, were (figs. 2 and 3) : band *a,* 476 and 503.5; band *b,* 477 and 504.5; band *c,* 477 and 507.5; band *d,* 477.5 and 507.5. These pigments all appear to be carotenes similar to lycopene (maxima, 477 and 507.5) and alpha-carotene (maxima, 476 and 507).

CAROTENOIDS OF THE FLIGHT FEATHERS OF C. CAFER

The feathers extracted were: rectrices, 29; primaries, 58; secondaries, 57; primary coverts, 49; secondary coverts, 77; alula feathers, 10. These were taken in about equal numbers from three adult males, one (orig. no. 433
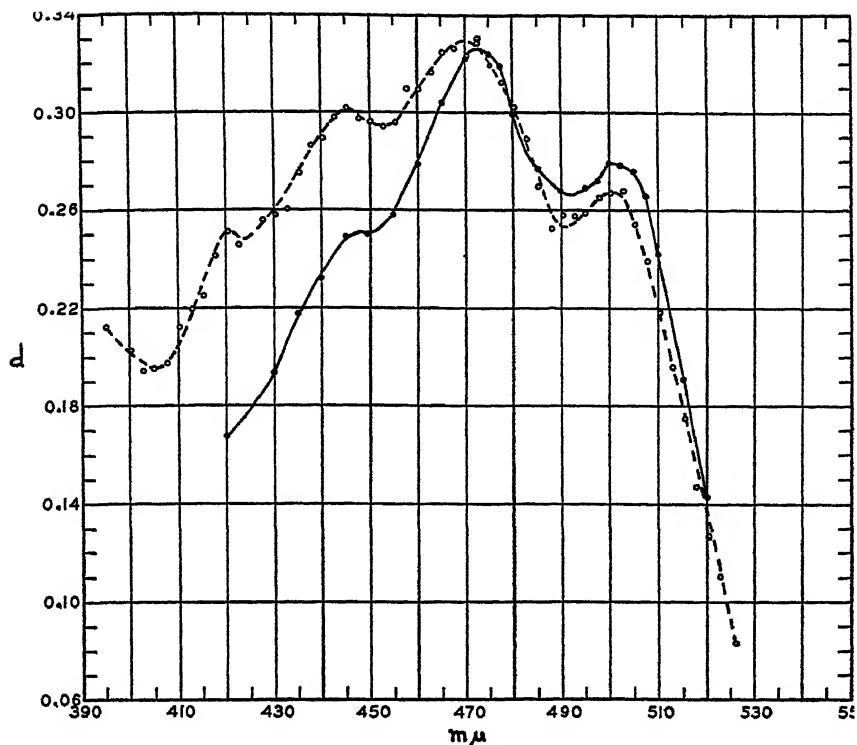
Fig. 1. Absorption curves of some hypophasic carotenoid pigments of the flight feathers of *Colaptes auratus*. Broken line, yellow-orange pigment *a*; solid line, yellow-orange pigment *b*. Ordinates, values of log I_0/I; abcissae, wave lengths.
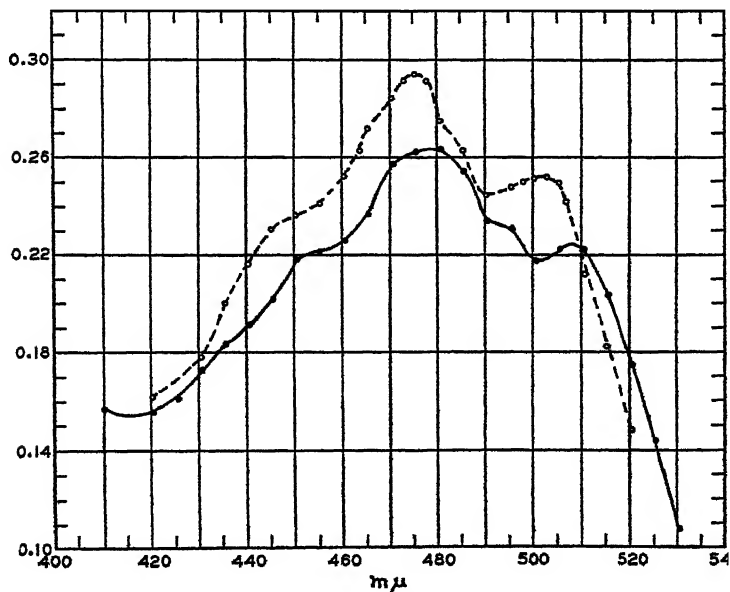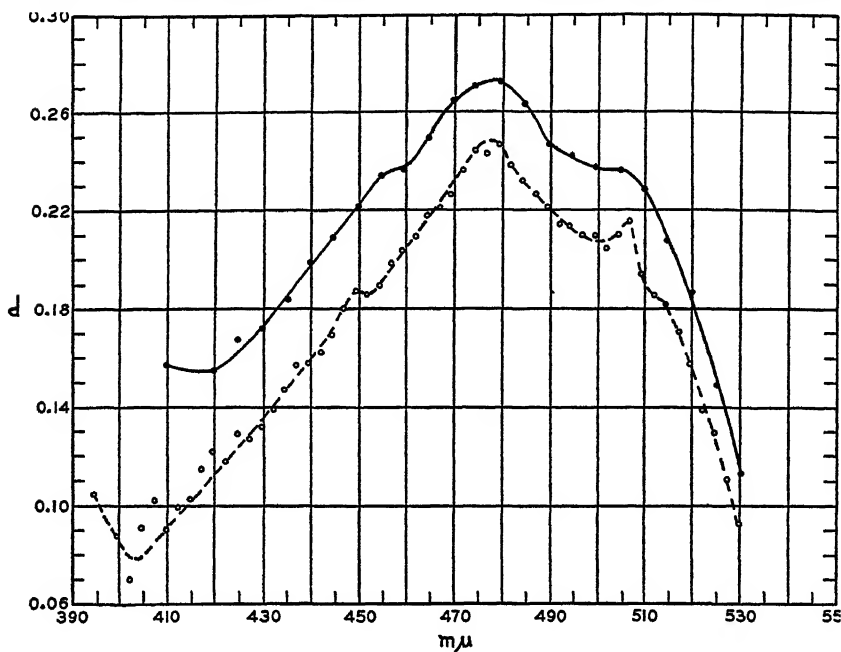

Fig. 2. Absorption curves of some epiphasic carotenoid pigments of the flight feathers of *Colaptes auratus*. Broken line, yellow pigment *a*; solid line, pigment *d*. Ordinates, values of log I_0/I; abcissae, wave lengths.

F.H.T.) taken near Los Altos, Santa Clara County, California, January 7, 1938, and the other two (orig. nos. 451 and 452 F.H.T.) taken at Davis, Yolo County, California, March 5, 1938. All these birds were typical of the species

Fig. 3. Absorption curves of some epiphasic carotenoid pigments of the flight feathers of *Colaptes auratus*. Solid line, orange pigment *b;* broken line, orange pigment *c.* Ordinates, values of log I_o/I; abcissae, wave lengths.

cafer except for one or two off-color feathers (not extracted) in two of them; the extracted feathers were scarlet.

Partition of the extract resulted in both the epiphase and the hypophase being highly colored. A chromatograph of the hypophasic fraction showed, from top to bottom, the following bands:

 a. A 28-mm. segment of pink, more intense at the bottom, in which two narrow orange bands were visible.
 b. Deep pink band 3 mm. wide.
 c. Orange band 3–4 mm. wide.
 d. Bright, intense pinkish red band 4 mm. wide.
 e. Bright yellow band 2 mm. wide.
 f. Pale orange band, rather diffusely spread over 4–5 mm.
 g. Rather pale pinkish orange band, also somewhat diffuse.

Bands *b, c, d,* and *e* were separated from each other by only narrow zones of colorless adsorbent. Band *f* was about 10 mm. below *e* and 7 mm. above *g.* Bands *a* and *b* were removed together; the others were removed separately.

The absorption curves of these hypophasic pigments in carbon disulfide, taken visually, show maxima as follows (figs. 4 and 5): band *c,* 465 or 475 mμ; band *d,* 490 mμ; band *e,* 476 and 507.5 mμ; band *f,* 460 and 485 mμ; band *g,* 495

mμ. Rechromatographing would have been necessary to separate bands *a* and *b* into their components, which probably were the same as the pigments forming the lower bands; this procedure was not carried out.
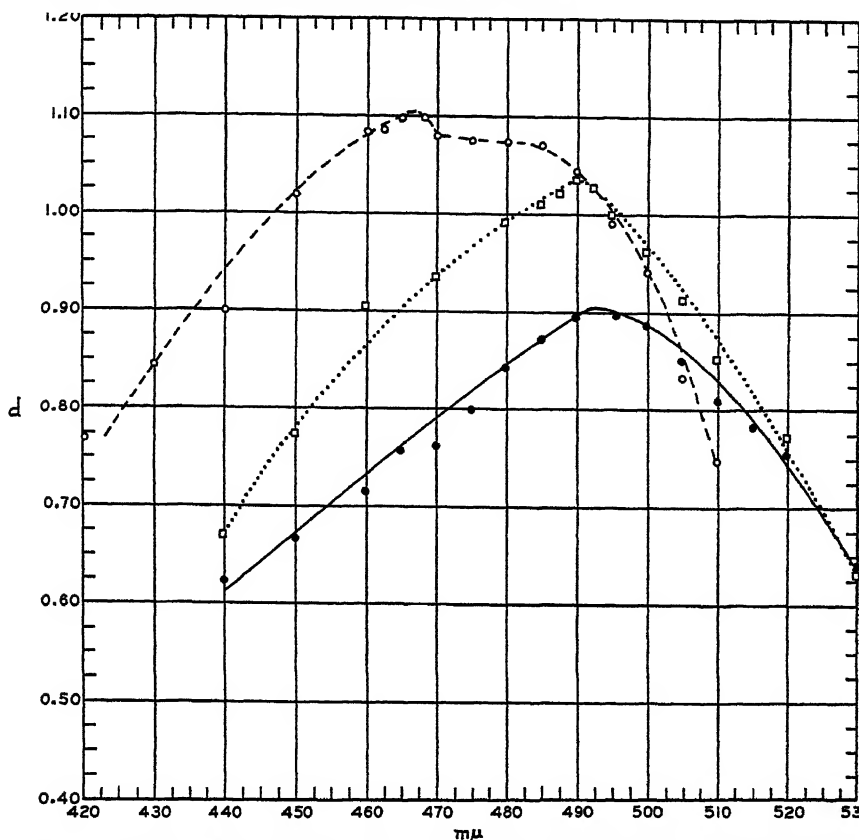

Fig. 4. Absorption curves of some hypophasic carotenoid pigments of the flight feathers of *Colaptes cafer*. Broken line, orange pigment *c;* solid line, pinkish orange pigment *g;* dotted line, pinkish red pigment *d.* Ordinates, values of log I_0/I; abcissae, wave lengths.

On the basis of such properties the pigments in these bands probably are to be identified as follows:

Band *c*. The curve obtained for this pigment is such that its shape is uncertain. The pigment may be one heretofore unknown, perhaps related to astacin or to the "Zersetzungsprodukte" found by Brockmann and Völker (1934:207) in the plumage of the male bullfinch, *Pyrrhula pyrrhula.*

Band *d*. Perhaps related to myxoxanthin (maximum, 489), or to astacin, or to the red pigment of *Pyrrhula pyrrhula.*

Band *e*. A xanthophyll, its absorption maxima most closely resembling those of lutein (475 and 508) and pentaxanthin (474 and 506).

Band *f*. This pigment shows a peculiar curve, and its identity is uncertain. Possibly it is a carotene not removed from the methanol in partitioning with petroleum ether. Strain (1938:20) lists an unnamed carotene, discovered by Karrer, Schöpp, and Morf, with maxima at 453 and 482 mμ.

Band *g*. Appears to be similar to astacin (maximum 500), or may be related to the red pigment of *Pyrrhula pyrrhula.*

The epiphasic fraction of the *cafer* extract was treated with alkali for 1¾ hours and the partition test applied. The major part of the pigment remained in the petroleum ether; most of that in the 90-per cent methanol could be extracted without further addition of water by shaking with petroleum ether. These extracts were added to the main epiphasic portion, and further treatment of the pigment with potassium hydroxide in 95-per cent ethanol was
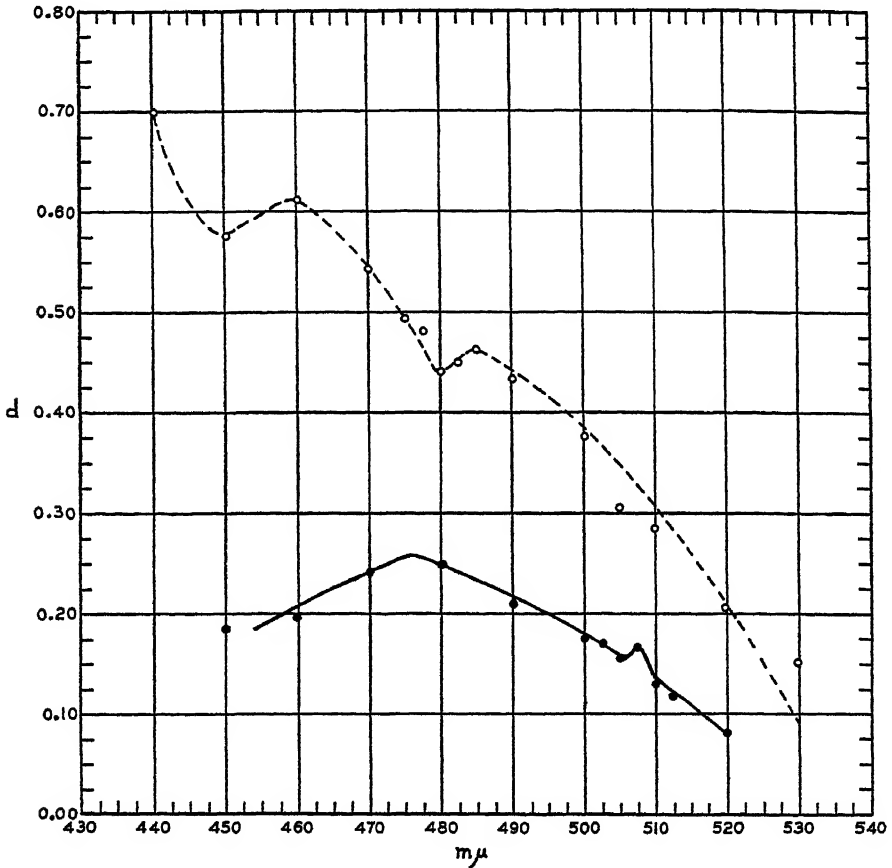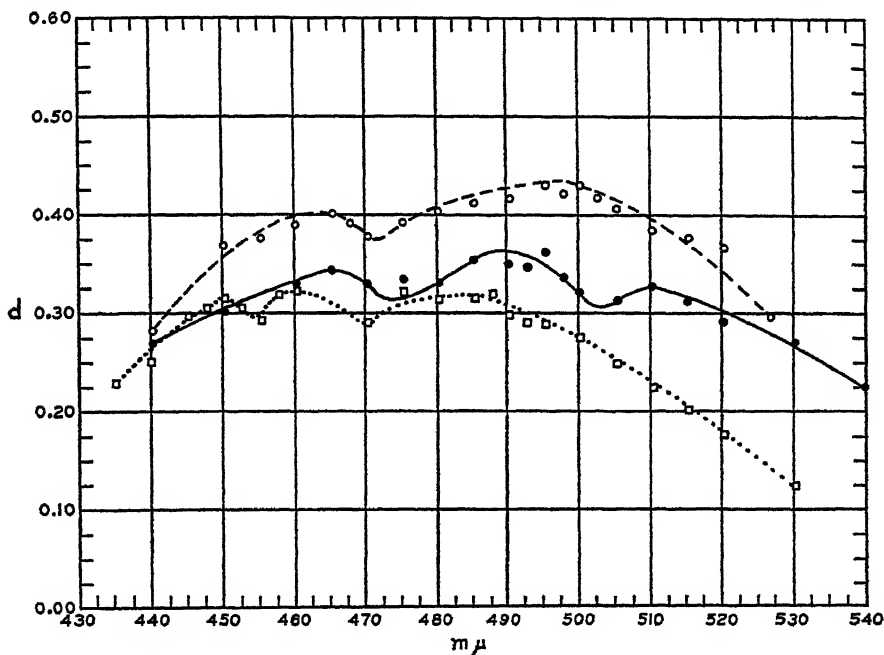

Fig. 5. Absorption curves of some hypophasic carotenoid pigments of the flight feathers of *Colaptes cafer*. Solid line, yellow pigment *e*; broken line, orange pigment *f*. Ordinates, values of log I_o/I; abcissae, wave lengths.

carried on for 3 hours. At the end of this time the partition test was applied again; the pigment still remained quantitatively in the petroleum ether.

This completely epiphasic pigment solution was chromatographed, with the following results. An orange band quickly separated from the rest of the pigment and, after repeated washing with petroleum ether, washed through into the filtering flask. This will be called band *e*. The remainder of the pigment was completely adsorbed and was washed with benzene for further separation of the bands.

The result, from top to bottom, was as follows:

a. Broad pink zone.
b. Orange-pink band some distance below.
c. Yellow band close to *b.*
d. Orange-red band close to *c.*

Each of these bands was dug out and eluted separately. Only part of band *a* could be eluted with petroleum ether and methanol; this was labeled a_1. Most of the remaining pigment of band *a* was eluted with carbon disulfide and called a_2.

The absorption curves of these pigments in carbon disulfide, made with a visual spectrophotometer, showed maxima as follows (figs. 6 and 7): band a_1,
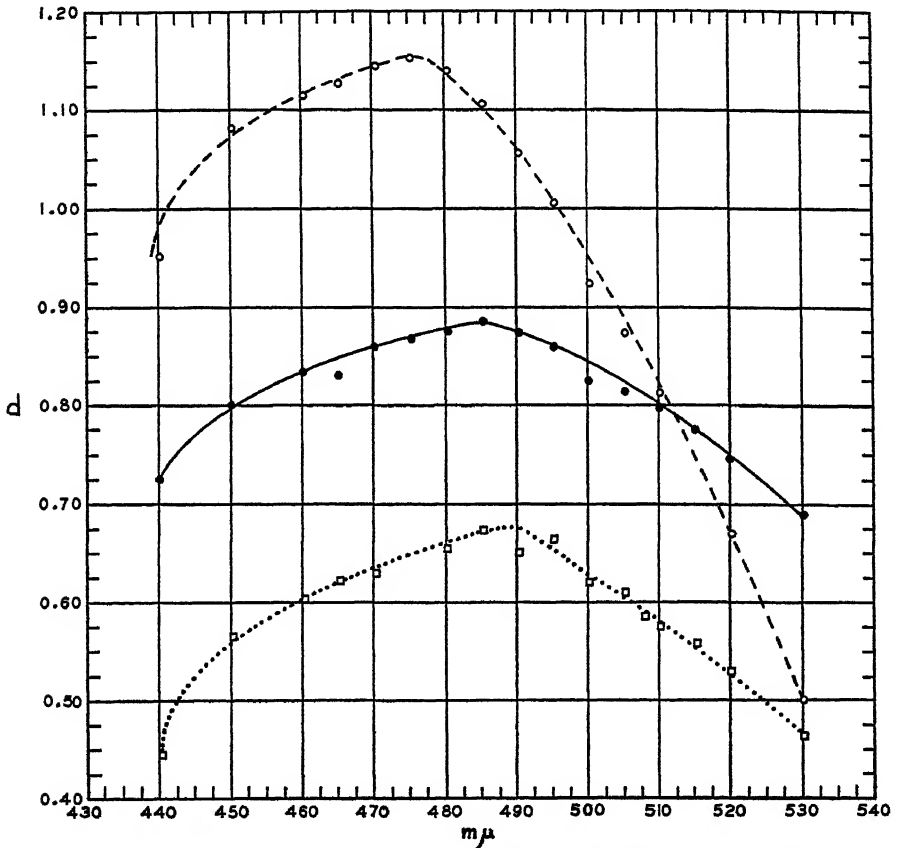

Fig. 6. Absorption curves of some epiphasic carotenoid pigments of the flight feathers of *Colaptes cafer*. Broken line, red pigment a_1; solid line, red pigment a_2; dotted line, yellow pigment *c*. Ordinates, values of log I_0/I; abcissae, wave lengths.

465 and 497.5 mμ; band a_2, 465, 490, and 510 mμ; band *b*, 485 mμ; band *c*, 450, 460, and 482.5 mμ, probably indicating a mixture of pigments; band *d*, 490 mμ; band *e*, 475 mμ.

Identification of the epiphasic pigments of *cafer:*

Band *a.* I am unable to identify this pigment satisfactorily. Its epiphasic solubility and its absorption maxima resemble gamma-carotene (maxima, 463 and 496 μ); the latter, however, is said not to be adsorbed on calcium carbonate.

Band *b.* ⎫
Band *d.* ⎬ Unknown pigments, probably similar to the "Zersetzungsprodukte" found by Brockmann and Völker.
Band *e.* ⎭

Band *c.* Probably a mixture of pigments, as noted above.

Carotenoids of Atypically Colored Flight Feathers

The carotenoid color of these feathers was yellow-orange, a hue that, presumably, was a direct or indirect result of interbreeding between *C. auratus* and *C. cafer*. The bird was closer to *cafer* in the sum of its characters but showed other atypical coloration in the brownish gray throat and in a slight brownish wash on the breast and sides. From this specimen (orig. no. 674 F.H.T., female, spring, 1938, San Jose, Santa Clara County, California) the

Fig. 7. Absorption curves of some epiphasic carotenoid pigments of the flight feathers of *Colaptes cafer*. Solid line, orange-red pigment *b*; dotted line, orange-red pigment *d*; broken line, orange pigment *e*. Ordinates, values of log I_0/I; abcissae, wave lengths.

following feathers were extracted: primaries, 10; secondaries, 11; rectrices, 5; tail coverts, 2; primary coverts, 3; secondary coverts, 6.

Partitioning resulted in the pigment being about evenly distributed between the petroleum ether and the methanol. A chromatograph of the hypophasic fraction exhibited the following bands, from top to bottom:

a. Two lemon yellow bands close together.
b. Two pale pink bands close together and about 8 mm. below bands *a*.
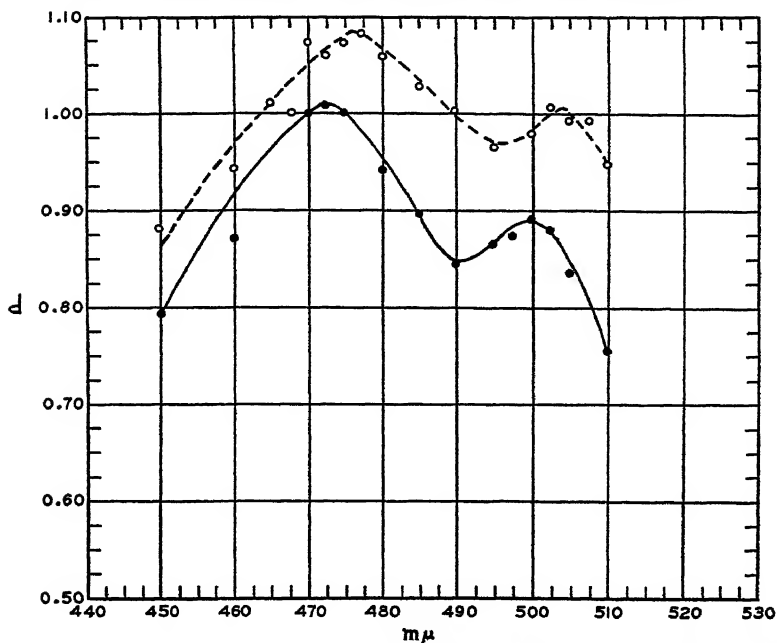*c.* Deep orange-yellow band several millimeters below bands *b*.

Fig. 8. Absorption curves of some hypophasic carotenoid pigments of the orange flight feathers of a "hybrid" *Colaptes*. Solid line, yellow pigment *a*; broken line, red pigment *b*. Ordinates, values of log I_o/I; abcissae, wave lengths.
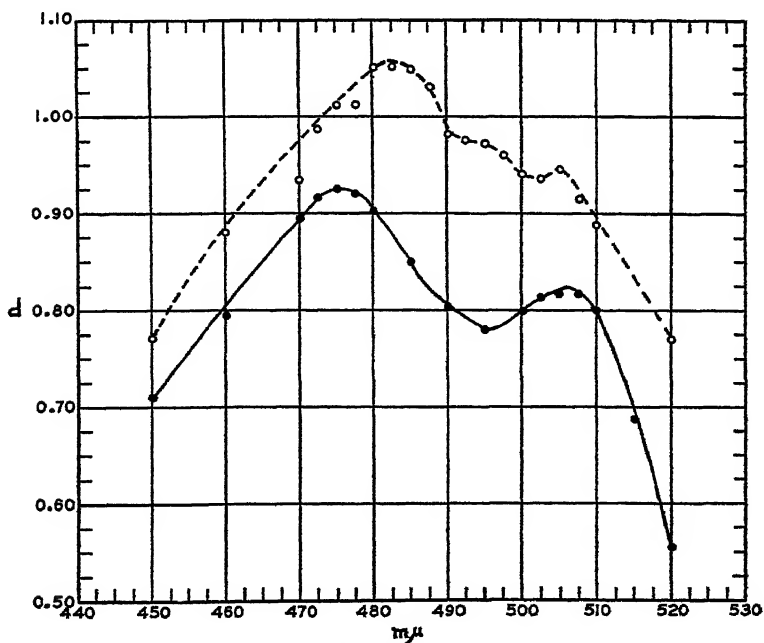

Fig. 9. Absorption curves of some carotenoid pigments of the orange flight feathers of a "hybrid" *Colaptes*. Solid line, orange-yellow hypophasic pigment *c*; broken line, yellow epiphasic pigment *b*. Ordinates, values of log I_o/I; abcissae, wave lengths.

Absorption curves determined for these pigments showed maxima as follows (figs. 8 and 9) : band *a*, 472.5 and 500 mμ; band *b*, 476 and 504 mμ; band *c*, 475 and 505 mμ.

These hypophasic pigments probably are to be identified as follows:

Band *a*. A xanthophyll, its maxima closest among known kinds to those of eloxanthin.

Bands *b* and *c*. Xanthophylls, perhaps closely related to lutein (maxima, 475 and 508 mμ) or to eschscholtzxanthin (475 and 503 mμ).
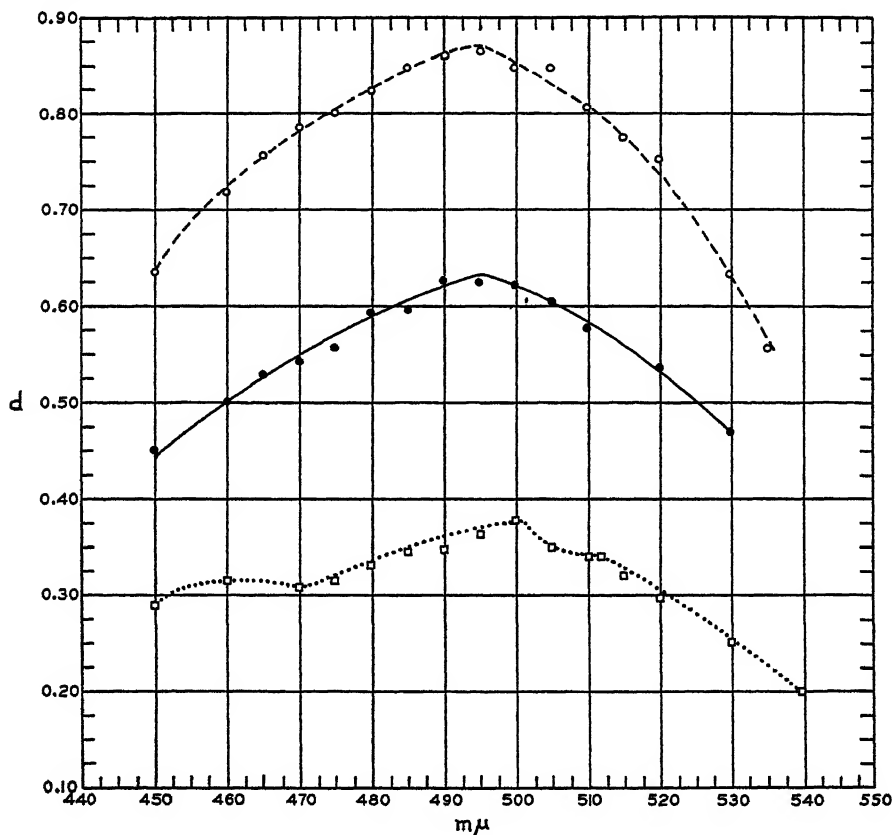

Fig. 10. Absorption curves of some hypophasic carotenoid pigments of the malar feathers of males of *Colaptes cafer*. Solid line, red pigment *a*; broken line, red pigment *d*; dotted line, red pigment *e*. Ordinates, values of I$_0$/I; abcissae, wave lengths.

The epiphasic fraction from the atypical feathers was hydrolyzed for five hours on a hot water bath but the pigment remained almost entirely epiphasic. A chromatograph showed the following bands:

a. Faint pink band near top of column.

b. Yellow band a short distance below *a*.

c. Faint pinkish band a considerable distance below *b*.

The only absorption curve determined (fig. 9), that of the pigment of band *b*, has a maximum at about 482.5 mμ and apparently a fainter maximum at 505 mμ. This pigment is perhaps a carotene. The pink bands, containing too little

pigment for determination of absorption curves, probably represent red pigments with single maxima, such as were found in *cafer*.

CAROTENOIDS OF MALAR STRIPE OF MALE C. CAFER

The extraction procedure was slightly modified for these feathers, which usually are less than a centimeter in length and have carotenoid only in the rami of the terminal one-half or one-third of the feather; their color is red. They were placed in a narrow-mouth bottle with a small quantity of methanol
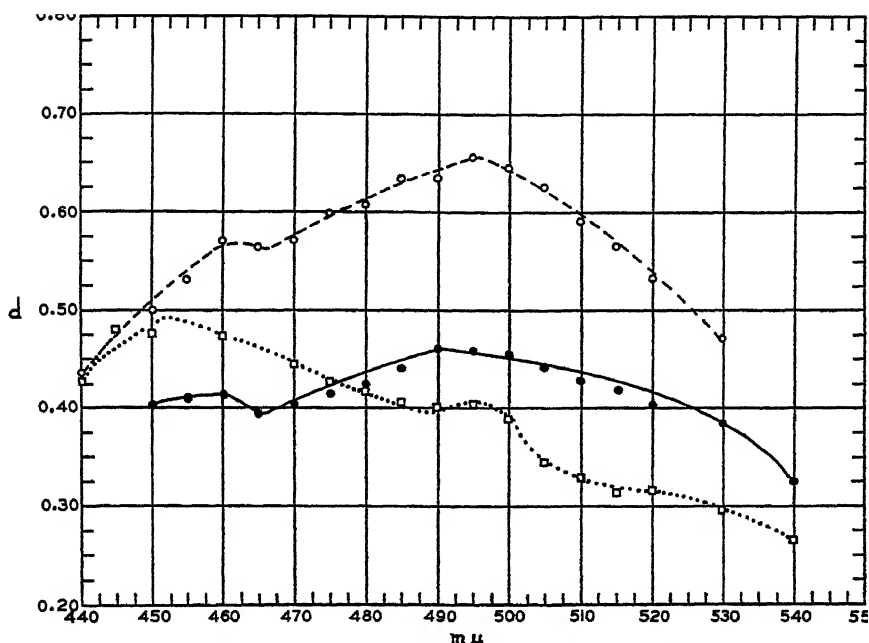

Fig. 11. Absorption curves of some carotenoid pigments of the malar feathers of males of *Colaptes cafer*. Broken line, yellow and red hypophasic pigments *b* and *c* together; solid line, red epiphasic pigment *b*; dotted line, yellow epiphasic pigment *e*. Ordinates, values of I_0/I; abcissae, wave lengths.

and several white glass marbles, and the ground glass stopper was wired in tightly. The bottle was placed in a horizontal position on two slightly irregular rubber rollers, and turned continuously for 84 hours, in the course of which time the extract was decanted twice and fresh methanol added. Most of the feathers were thus reduced to a fine powder; the others were strongly worn and very pale orange.

The malar feathers from seven males of *C. cafer*, collected at Davis, Yolo County, and Clayton, Contra Costa County, California, on March 4, 5, and 8, 1938, were extracted. Partition of the extracted pigment between petroleum ether and 90-per cent methanol showed the largest part of the pigment to be hypophasic.

A chromatograph of the hypophasic fraction gave only a single orange-pink band at the top of the column until washed with benzene, when the pigment

formed four or five bands, all near the top of the column and adjacent to one another. These are, from top to bottom:

  a. Red band at top of column.
  b. Zone of pale yellow.
  c. Red band, slightly orange in hue.
  d. Pink-red band, much more intensely colored than the others.
  e. Diffuse zone of pink.

TABLE 1

PROPERTIES OF HYPOPHASIC CAROTENOIDS OF MALAR FEATHERS OF MALES OF C. CAFER

Band	Color of pigment adsorbed on CaCO₃	Color of CS₂ solution	Absorption maxima (mμ) in CS₂	
a	Red...........................	red		495
b	Yellowish ⎰ eluted	red	460	
c	Red (slightly orange) ⎱ together		(Weak)	495
d	Pink-red.....	red		495
e	Pink.............................	red	460	500
			(Weak)	

The properties of these hypophasic pigments are summarized in table 1 (see figs. 10 and 11 for absorption curves).

From these data it seems that the principal hypophasic pigments are red with single absorption maxima, which in three pigments are at 495 mμ, and in

TABLE 2

PROPERTIES OF EPIPHASIC CAROTENOIDS OF MALAR FEATHERS OF MALES OF C. CAFER

Band	Color of pigment adsorbed on CaCO₃	Color of CS₂ solution	Absorption maxima (mμ) in CS₂	
a	Pink.............................	....		...
b	Red..........	red	460	495
			(Weak)	
c	Orange......	....		...
d	Orange (weakly adsorbed)..........	....		...
e	Yellow (weakly adsorbed)..........	yellow	452.5	495

one is at 500. The weak absorptions found at 460 and 465 mμ probably result from traces of unseparated xanthophylls, the second maxima of which are masked by the broad, strong absorption of the red pigments in solution with them.

No attempt was made to hydrolyze the epiphasic fraction of malar pigments; they formed a chromatograph of three bands when washed with petroleum ether. At the top was a broad, pink band, and slightly below it a narrow red band, both strongly adsorbed; a yellow band moved slowly down the column but at about 20 mm. became too diffuse and faint to be followed further. Developing with benzene gave, in sequence from top to bottom, the following bands.

a. Pink band, close to top of column.
b. Red band, narrow, 2 mm. below *a.*
c. Orange band, just below *b.*
d. Orange band, 30 mm. below *c;* probably would have washed completely through had washing been continued a little longer.
e. Yellow band, 3 mm. below *d;* washed through into filter flask.

The properties of the pigments in these bands are given in table 2. Some pigments were present in amounts too small for determination of absorption curves; the two curves obtained are reproduced in figure 11.

These data indicate that two, and perhaps three, types of pigment were in this epiphasic fraction. Bands *a* and *b* both probably contain a red pigment with a single absorption maximum at or near 495 mμ. Band *b* apparently contains also a trace of xanthophyll ester, producing the weak absorption at 460 mμ. Band *c* may also contain a xanthophyll ester. Bands *d* and *e*, being adsorbed so weakly on the calcium carbonate, may be carotenes.

CAROTENOIDS OF NUCHAL CRESCENT OF C. AURATUS

Insufficient material was available to give satisfactory data on these pigments. However, both epiphasic and hypophasic fractions were found, and their chromatographs were similar to those obtained with the malar feathers of males of *cafer*. The three absorption curves that were obtained show a comparable likeness.

CONCLUSIONS

The identifications here reported for the carotenoid pigments of certain feathers of three kinds of flickers (*Colaptes*) must be considered to be tentative. Certain general conclusions may, however, be drawn.

The red, orange, and yellow colors of the feathers of *C. auratus, C. cafer,* and hybrids between these species are caused by mixtures of carotenoid pigments. These pigments belong to three classes: (1) xanthophylls, principally in free form but to at least some extent esterified; (2) carotenes, present in much smaller amounts than are the xanthophylls; (3) red carotenoids, both epiphasic and hypophasic, each exhibiting a single absorption maximum at some point in the region of the spectrum between 475 mμ and 500 mμ.

The yellow color of *C. auratus* (and probably, the yellow of *chrysocaulosus* and *chrysoides*) results principally from xanthophylls, and to a lesser extent from carotenes. The scarlet of *cafer* is produced in largest part by the red pigments of class 3 above, but the presence of xanthophylls and carotenes like those of *auratus* makes the color more yellowish than it probably would be otherwise. *C. cafer,* then, has a greater number of pigments than *auratus,* and its specific coloration results from the addition of new pigments rather than by total replacement of the kinds which occur in *auratus.* Flight feathers of hybrids intermediate in color between red and yellow also contain all three classes of pigments mentioned above, but apparently in different proportions than occur in typically red feathers of *cafer,* the red pigments forming a smaller percentage of the total. Hybrids, therefore, possess the types of pig-

ments found in both parental species, as might be expected since all types exist in *cafer*. By analogy, the orange-red flight feathers of *C. mexicanoides* probably contain a mixture of pigments similar to that of *cafer,* but with less of the reds.

The red pigments of the malar feathers of *cafer* (and probably also of all other species of *Colaptes*) and those of the nuchal crescent of *auratus* (and probably *chrysocaulosus*) are mostly red hypophasic carotenoids with single absorption maxima. In addition, both kinds of feathers contain some epiphasic red pigment and small amounts of xanthophylls and perhaps carotenes.

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TWO NEW SUBSPECIES OF KANGAROO RATS (GENUS DIPODOMYS) FROM SOUTHERN CALIFORNIA

BY

JEAN T. BOULWARE

TWO NEW SUBSPECIES OF KANGAROO RATS (GENUS DIPODOMYS) FROM SOUTHERN CALIFORNIA

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(Contribution from the Museum of Vertebrate Zoölogy of the University of California)

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In the course of field work in the past three years, Dr. Richard M. Bond of the Soil Conservation Service of the United States Department of Agriculture collected kangaroo rats in southwestern San Luis Obispo County and western Santa Barbara County, California. Dr. Bond was interested in identifying the species because kangaroo rats had not been recorded from this area, and because in some places they are known to have an appreciable effect upon soils. When the specimens were examined at the Museum of Vertebrate Zoölogy, they were found to differ from the kinds of kangaroo rats recognized in adjacent areas and, with Dr. Bond's generous consent, were turned over to me for detailed study.

The specimens include representatives of two species: *Dipodomys heermanni* and *Dipodomys agilis*. In western Santa Barbara County the two species are almost indistinguishable at first glance. However, study shows that they may be separated on the basis of a number of characteristics.

The length and curvature of the os penis, or baculum, readily differentiates the two species. The baculum of *heermanni* is longer and curves downward more abruptly at the distal end than that of *agilis*. In adult *heermanni* from Davis Ranch, Santa Barbara County (nos. 84841, 89905, and 84842, Mus. Vert. Zool.), the bacula are 11.1 mm., 11.6 mm., and 12.0 mm. long, respectively. In adult *agilis* from La Purisima Mission in the same county (nos. 84846 and 84845), the bacula are 9.8 mm. and 9.9 mm. long. Measurements were taken with the jaws of the calipers held at right angles to the shaft of the bone. Corresponding differences in length and shape of the bacula of *D. heermanni swarthi* and *D. a. agilis* are shown in drawings by Burt (1936:154, fig. 5).

As measured from the anterior alveolar border of the fourth premolar to the posterior alveolar border of the third molar, the maxillary tooth row is uniformly longer in *heermanni* than in *agilis*. Length of tooth row in five adult males of *heermanni* averages 5.2 mm. (5.1–5.3 mm.); in three adult males of *agilis*, 4.7 mm. (4.6–4.8 mm.).

The dark facial crescents of *heermanni* are more sharply angled, and the area of light hairs extending up beside either nostril is correspondingly narrower than in *agilis*; the facial crescents of *agilis* arch more broadly, and the light area below each crescent is wider. In *heermanni* this area is white; in *agilis* the hairs on the anterior edges of the dark crescents are buffy.

On the basis of materials from outside the Santa Barbara area, Grinnell (1922: 26) pointed out several differences between the skulls of the two species. Of these differences the following hold for specimens from the area under consideration. In *heermanni* the skull is "broad-faced," that is, the maxillary arches spread apart broadly from the long axis of the skull, the maxillary plate of the zygomatic arch

is broad at the middle, and the postero-external angle of the maxillary plate is sharp and prominent. In *agilis* the skull is "narrow-faced," the maxillary arches do not spread widely, the maxillary plate is narrow at the middle, and the postero-external angle is weakly developed. The auditory bullae of the "broad-faced" *heermanni* are relatively small, with the result that the skull is squarish in dorsal aspect, whereas the narrow arches and greatly inflated bullae of *agilis* give the skull a triangular appearance. A difference not pointed out by Grinnell, but perhaps correlated with this inflation of the bullae, is that the anterior part of the basioccipital is more expanded in *agilis* than in *heermanni*.

In dorsal aspect *agilis* is slightly darker and duller than *heermanni*. Comparative dorsal color seems more dependent here upon length and density of pelage (longer and less dense in *agilis* than in *heermanni*) than upon pigmentation. The buffy subterminal bands and the black tips of the dorsal hairs are of similar lengths in both species, but the plumbeous basal portions in *agilis* are longer and therefore contribute more gray to the color of the dorsum. This darkening and dulling effect is augmented by the less dense pelage and the less intense color of the subterminal bands in *agilis*.

Other external differences, also of an average sort, are present in the two species. In *heermanni*, as compared with *agilis*, the ear is smaller, the hind foot shorter, and the hairs at the fold of the pinna usually white, rather than either buffy or indistinguishable in color from the remainder of the pinna.

The specimens of *D. heermanni* were all taken in open, sandy areas, relatively free of chaparral. Most of the *D. agilis* were collected in a low stand of mixed chaparral. The soil here is derived from an underlying diatomaceous shale, which is heavier than sand and bears some resemblance to clay. One specimen of *agilis* was taken in an open, sandy area along with *heermanni*.

In this paper, specimens are considered adult if all three of the following conditions exist: pelage adult; bone of skull of fine texture and bullae somewhat transparent; upper third molar worn sufficiently so as to lack, or nearly lack, an indentation on its posterolingual margin.

The cranial measurement designated as *width of supraoccipital* is the distance across the supraoccipital between the two points at which the mastosupraoccipital sutures are met by the sulci which extend dorsally and then medially from the posterior border of the auditory meatus (see Howell, 1932: 494). *Length of bulla* is taken by placing one jaw of the calipers in the mastosquamosal suture just below the posterolateral part of the parietal, and the other jaw of the calipers at the posteriormost point of the bulla. Measurements of *greatest length* and *width of maxillary arch at middle* are taken in the manner described by Grinnell (1922: 4–6). Other cranial measurements are as illustrated by Hall and Dale (1939: 50, fig. 2).

All specimens mentioned are in the Museum of Vertebrate Zoölogy. Capitalized color terms are those of Ridgway's "Color Standards and Color Nomenclature" (1912).

I am indebted to Professors E. Raymond Hall and Seth B. Benson for critical supervision and assistance in the preparation of this report.

Dipodomys heermanni arenae, new subspecies

Type.—Male, adult, no. 84840, Mus. Vert. Zoöl.; C. A. Davis Ranch, 2 mi. NNW Lompoc, 400 ft., Santa Barbara County, California; collected February 16, 1939, by Richard M. Bond; original no. 127.

Range.—The Pacific slope of San Luis Obispo and Santa Barbara counties from Oceano southward to the Santa Inez River and up the Santa Inez River valley at least as far as Buellton.

Diagnosis.—A medium-sized race of *Dipodomys heermanni* characterized by dark dorsal color,

occasional obscuration or incompleteness of the white hip stripe, and small bullae. Basal portion of dorsal hairs near Deep Mouse Gray (10'''' *j*); subterminal band near Pinkish Cinnamon (15'' *a*); tip black.

Measurements.—Average and extreme measurements in millimeters of 5 adult males and 7 adult females, all from Davis Ranch and 2.4 mi. W Buellton, are as follows: Length of body, ♂, 121 (113–126), ♀, 118 (115–122); length of tail, 177 (171–185), 171 (144–181); length of hind foot, 41.6 (40–43), 41.4 (40–44); ear from notch, 16.1 (15–17), 16.1 (15–17). *Skull:* Greatest length, 39.7 (38.6–40.5), 39.5 (38.4–41.0); basal length, 28.2 (27.7–28.7), 28.1 (27.2–29.3); breadth across bullae, 24.7 (24.3–25.2), 24.4 (23.2–25.1); maxillary breadth, 22.6 (21.8–23.2), 21.9 (21.5–22.4); length of bulla, 13.4 (12.9–13.7), 13.2 (12.5–13.8); width of maxillary arch at middle, 5.2 (4.9–5.4), 5.0 (4.9–5.2); width of supraoccipital, 2.1 (2.0–2.4), 2.3 (1.6–2.7); length of nasal, 14.8 (14.2–15.3), 14.7 (14.2–15.7). Weight in grams of 2 adult males and 6 adult females: ♂, 86.0, 76.7; ♀, 66.7 (59.5–73.8).

Specimens examined.—Total number, 29, all from California. *San Luis Obispo County:* 2¾ mi. S Oceano, 10 to 50 ft., 15. *Santa Barbara County:* C. A. Davis Ranch, 2 mi. NNW Lompoc, 400 ft., 11; 2.4 mi. W Buellton, 350 ft., 3.

Comparisons.—As compared with *D. h. jolonensis* and *D. h. swarthi, arenae* differs as follows: Dorsal color distinctly darker, and blackish rather than brownish; arietiform facial crescents heavier and blacker; hairs in tuft of tail black for nearly half their length rather than tipped with brownish black for one-fourth their length; hind foot smaller; auditory bullae smaller. Upper incisors slightly shorter than in *swarthi.* Supraoccipital wider than in *jolonensis.*

As compared with *morroensis:* Dorsal color lighter; ears less blackish and with a greater number of white hairs at the fold of the pinna and at the lateral base of the pinna; dorsal tail stripe lighter; white hip stripe sometimes obscured or incomplete, rather than characteristically incomplete or absent; cranium less highly arched; bullae more inflated; supraoccipital narrower; maxillary breadth 91 per cent as opposed to 94 per cent of breadth across bullae.

Remarks.—Study of specimens of *arenae* prompts a reconsideration of the systematic status of *Dipodomys morroensis,* heretofore regarded as a full species (Grinnell, 1922). In the present paper, *morroensis* is treated as a subspecies, *Dipodomys heermanni morroensis,* because *arenae* has characters which are intermediate between *morroensis,* on the one hand, and *D. h. jolonensis* and *D. h. swarthi,* on the other hand. *Dipodomys h. jolonensis* differs from *swarthi* chiefly in darker coloration and in an intensification of dark markings. The dark coloration is further intensified in *arenae* and reaches an extreme in *morroensis.* The skull of *arenae* is intermediate between the small skull of *morroensis* and the large skulls of *jolonensis* and *swarthi* in degree of inflation of bullae, width of supraoccipital, and length of nasal.

Dipodomys agilis fuscus, new subspecies

Type.—Male, adult, no. 84845, Mus. Vert. Zoöl.; 2½ mi. N La Purisima Mission, 600 ft., Santa Barbara County, California; collected February 16, 1939, by Richard M. Bond; original no. 162.

Range.—Known only from the vicinity of Lompoc, Santa Barbara County, California.

Diagnosis.—A long-bodied race of *Dipodomys agilis* characterized by dark dorsal color, relatively small ears, and large bullae. Basal portion of dorsal hairs about Deep Mouse Gray (10'''' *j*); subterminal band Light Pinkish Cinnamon (15'' *a*); tip black.

Measurements.—Average and extreme measurements in millimeters of 3 adult males, one of which is from Davis Ranch, and 1 adult female, are as follows: Length of body, ♂, 125 (121–129), ♀, 119; length of tail, 171 (151–181), 172; length of hind foot, 43 (42–44), 43; ear from notch, 16.3 (16–17), 16. *Skull:* Greatest length, 40.9 (40.2–41.3), 40.6; basal length, 28.7 (28.5–28.9), 28.3; breadth across bullae, 25.7 (25.5–25.9), 26.1; maxillary breadth, 21.5 (21.2–21.7), 21.5; length of bulla, 14.5 (14.3–14.8), 14.9; width of maxillary arch at middle, 4.7 (4.6–4.8), 5.1; width of supraoccipital, 2.2 (2.1–2.3), 2.1; length of nasal, 14.8 (14.3–15.6), 14.5.

Specimens examined.—Total number, 4, all from *Santa Barbara County,* California: 2½ mi. N La Purisima Mission, 600 ft., 3; C. A. Davis Ranch, 2 mi. NNW Lompoc, 400 ft., 1.

Comparisons.—As compared with *D. a. agilis, D. a. fuscus* differs as follows: Dorsal color darker; yellow-orange of sides paler; arietiform facial markings heavier, and black rather than brownish; pelage longer; body longer; ear smaller; skull longer; auditory bullae larger; maxillary breadth 84 per cent as opposed to 88 per cent of breadth across bullae. A skull of *fuscus* (no. 84845, ♂) and one of *agilis* (no. 6932, ♂) both have a basal length of 28.9 mm. and a maxillary breadth of 21.7 mm. In the former, however, breadth across bullae is 25.9 mm. and the length of bulla is 14.8 mm., whereas the measurements are only 24.6 mm. and 13.6 mm. in the latter.
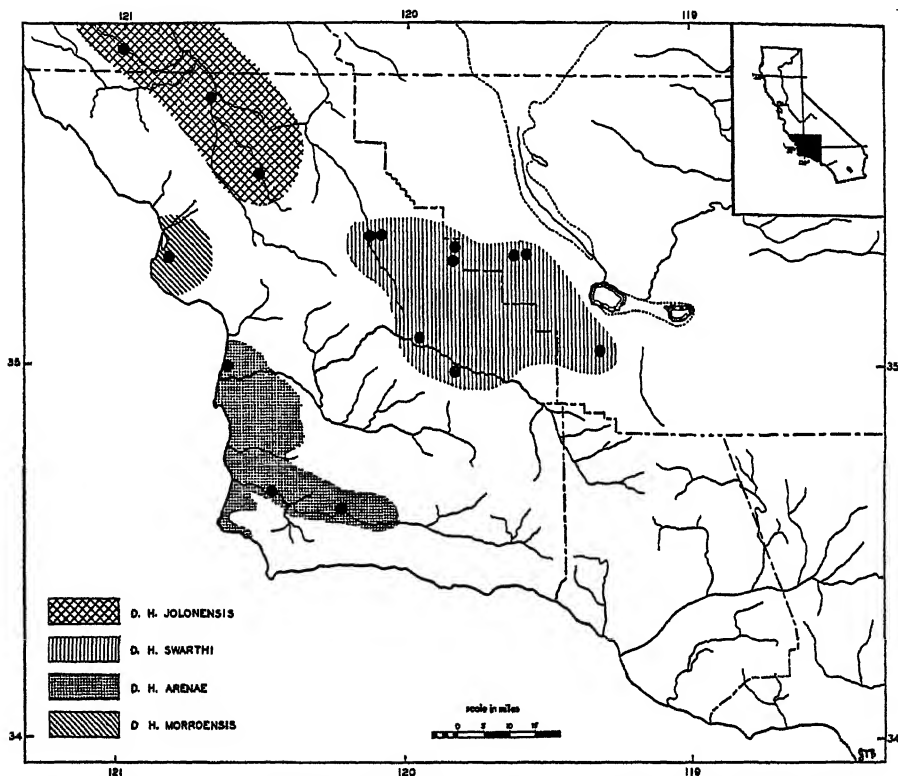

Fig. 1. Map showing the geographic distribution of four subspecies of *Dipodomys heermanni.*

As compared with *D. a. perplexus:* Dorsal color darker; arietiform facial marking heavier and blacker; dorsal and ventral tail stripes darker and wider; hind foot shorter; ear smaller; bullae larger and, as viewed laterally, sloping off less steeply in back of the frontoparietal sutures; angular process of the mandible shorter.

As compared with *Dipodomys venustus sanctiluciae:* Dorsal color darker; yellow-orange of sides paler; hind foot shorter; ear smaller; teeth smaller; skull smaller in all measurements taken, except for bullae. The larger bullae of *fuscus* give its skull a more triangular appearance in dorsal aspect than the skull of *sanctiluciae.*

Remarks.—*Dipodomys a. fuscus* occurs in what formerly was considered a part of the range of *D. a. agilis.* Grinnell (*op. cit.,* p. 92, fig. W) assumed that the range of *agilis* included the whole of Santa Barbara County. This supposition presumably was made upon the basis of one specimen from the Cuyama Valley in the extreme

northeastern part of the county and upon geographical information then at hand.
The occurrence of *fuscus* in western Santa Barbara County still leaves the possibil-
ity that *agilis* may extend northward into the eastern part of the county. The speci-
men available to Grinnell (no. 16673, ♀, from Schoolhouse Canyon, Cuyama Valley),
however, now seems an inadequate basis upon which to make this assumption. This
lone specimen is not clearly representative of *agilis*, a fact recognized by Grinnell
who wrote "not typical" on the label. The specimen in question, while differing
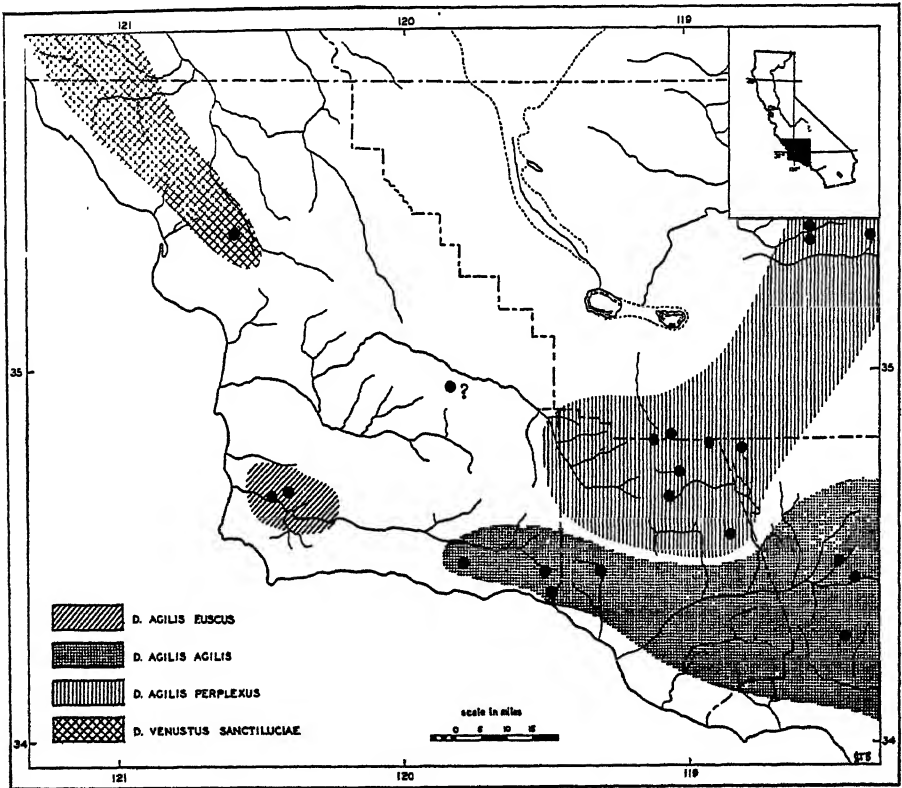from *agilis* in smaller hind foot, smaller ear, and greater breadth across bullae,

Fig. 2. Map showing the geographic distribution of one subspecies of *Dipodomys venustus* and
three subspecies of *Dipodomys agilis*.

differs even more from *D. a. fuscus* and *D. a. perplexus*. Neither does it have the
characters of *D. h. swarthi* or *D. ingens* which occur in the Cuyama Valley. For the
present I leave this specimen unassigned.

The westernmost point in the range of *D. a. agilis* as now known is near San Jose
Creek in southeastern Santa Barbara County. A juvenal specimen from "San
Marcos Road," near San Jose Creek, made available to me by Mr. Egmont Z. Rett,
from the Santa Barbara Museum of Natural History, seems referable to *agilis*,
although its color is intermediate between that of *agilis* and *fuscus*. Kangaroo rats
that Dr. Bond collected two miles east of Carpinteria also approach *fuscus* in color,
but otherwise may be assigned to *D. a. agilis*.

Grinnell (*op. cit.*, p. 100) pointed out the possibility that intergrades between
D. v. sanctiluciae and *D. a. perplexus* might be found in the territory intervening
between the ranges of these two forms, in which event it would be best to consider

D. v. venustus and *D. v. sanctiluciae* as subspecies of *agilis*. This conjecture was based on the apparent trend of increase in the size of the ear toward the north among the members of the *agilis* group. It might be expected, then, that *fuscus*, whose range is between those of *sanctiluciae* and *agilis* and west of that of *perplexus*, would approach *sanctiluciae* and *perplexus* in large size of ear. This is not so, for *fuscus* has a smaller ear than *agilis*. This situation does not, however, preclude the possibility that *sanctiluciae* and *perplexus* may yet be found to intergrade in the area northeast of the range of *fuscus* and at higher elevation.

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